

FINAL REPORT

Development of Adaptive Management Tools to Guide Habitat Allocations for At-Risk Species

SERDP Project RC-1656

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14. ABSTRACT The Department of Defense is increasingly engaging landowners outside installation boundaries to help protect biodiversity at a landscape scale. Such activities include the acquisition of recovery habitat for species at risk and cooperation with conservation partners. The objectives of this project were to 1) contrast the ability of data provided by different conservation partners to reduce uncertainty in dynamic landscape simulation models (i.e., individual-based, spatially explicit population models, IB-SEPMs); 2) apply Decision Analysis to identify the most cost-effective allocation of habitat, given uncertainty in the IB-SEPM; and 3) contrast the ability of the technique to be applied to well-studied (i.e., red-cockaded woodpecker) and poorly-studied (gopher tortoise) species. The study found that the natural history of the red-cockaded woodpecker was sufficiently understood to prioritize habitat allocations to protect the abundance of the species but not to protect genetic diversity of the species. In contrast, for the gopher tortoise this study concluded that we do not sufficiently understand the species natural history traits to protect either abundance or genetic diversity. The methods developed here provide an approach for managing habitat area and connectivity that includes uncertainty regarding species natural history, helps to prioritize collection of monitoring data, and supports cost-effective decision making.					
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List of Acronyms

A_i	Number of unique alleles per breeding group
ACUB	Army Compatible Use Buffer
CL	Marine Corps Base Camp Lejeune
CNF	Croatan National Forest
Conn	Connectivity
D_{ij}	Minimum pair wise genetic distance
DoD	Department of Defense
DSS	(RCW) Decision Support System
D_{ST}	Increase in genetic divergence among territories
EP	Encroachment Partnering
EV	Expected Value
EVPI	Expected Value of Perfect Information
F	Female
FB	Fort Benning
F_{ST}	Proportion of total genetic variation due to population subdivision
Group	Group size
GT	Gopher tortoise
H_S	Average genetic diversity within breeding groups
HS	Holly Shelter State Game Lands
H_T	Genetic diversity estimated at the population level
IAM	Infinite Alleles Model
IB-SEPM	Individual-based, spatially explicit population model
LEA	Landscape Equivalency Analysis
LiDAR	Airborne Laser Altimetry
LSY	Landscape Service Year
M	Male
N_e	Effective population size
ODD	Overview, Design concepts, and Details
OMPG	One Migrant Per Generation
PBG	Potential Breeding Group
POM	Pattern Oriented Modeling
RCW	Red-cockaded woodpecker
SERDP	Strategic Environmental Research and Development Program
SSq	Sum of squares
TNC	The Nature Conservancy

Keywords:

individual-based, spatially-explicit population model, inverse parameterization, dynamic landscapes, Encroachment Partnering, Army Compatible Use Buffer Program, landscape genetics, habitat loss and fragmentation, red-cockaded woodpecker, gopher tortoise, resource-based compensation, cost-effectiveness analysis, Decision Analysis, Camp Lejeune, Ft. Benning

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Abstract

Objectives. The Department of Defense (DoD) is increasingly engaging landowners outside installation boundaries to help protect biodiversity at a landscape scale. Such activities include the acquisition of recovery habitat for species at risk. SERDP Exploratory Development (SEED) project RC-1469 evaluated how such habitat allocations would affect population viability for the red-cockaded woodpecker (*Picoides borealis*, RCW) on Marine Corps Base Camp Lejeune. As an extension of that research, this project evaluated the contribution different data types make to reducing uncertainty in individual-based, spatially explicit population models (IB-SEPMs), and, given this uncertainty, what is the most cost-effective allocation of habitat. In contrast to the SEED project, this project increased the spatial scale of analysis for RCWs across the greater Onslow Bight landscape, while incorporating data from conservation partners to help reduce uncertainty in RCW population dynamics. This project also illustrated the transferability of the techniques to lesser known species by applying them to the gopher tortoise (*Gopherus polyphemus*, GT), at Fort Benning (FB), including their associated Army Compatible Use Buffer (ACUB) lands.

Technical Approach. Habitat management often entails tradeoffs among habitats at different locations and at different times. Both the spatial location and timing of land use change can affect the realized conservation benefit associated with such decisions. IB-SEPMs have a proven ability to predict biological patterns in dynamic landscapes. Military installations will often wish to change habitat allocations prior to reaching a scientific consensus regarding the behavior and demography of at-risk species; therefore Decision Analysis, a structured approach for contrasting alternative habitat allocations given uncertainty in system dynamics (e.g., dispersal and/or reproduction), is applied. This requires applying two techniques to IB-SEPMs. The first is Pattern Oriented Modeling (POM), a retrospective analysis that evaluates uncertainty in IB-SEPMs. The second simulation modeling technique is Landscape Equivalency Analysis (LEA), which estimates credits and debits that reflect changes in abundance and genetic variation toward sustainability criteria. By incorporating genetic criteria, LEA recognizes that the amount of migration required to minimize the influence of inbreeding, genetic drift, and local extinction will vary as landscape patterns change over time.

Decision Analysis for RCWs was applied using an IB-SEPM for the Coastal NC Recovery population, which includes Holly Shelter State Game Lands (HS), Croatan National Forest (CNF), and Marine Corps Base Camp Lejeune (CL). A habitat model was constructed for the one million hectare landscape and RCW monitoring data were collected from all stakeholders. POM was applied to contrast the ability of monitoring data to reduce uncertainty in the dispersal submodel of the IB-SEPM. The five most plausible dispersal parameterizations were then used to evaluate six alternative habitat allocations for the Onslow Bight landscape using LEA.

To illustrate the transferability of the POM/LEA technologies to a lesser known species, an IB-SEPM was constructed for the GT. This was accomplished by performing an extensive literature review, constructing a habitat model, and conducting a landscape genetic study at FB. All available monitoring data were collected through collaboration with FB, The Nature

Conservancy (TNC), and Auburn University. Therefore, we were able to apply POM to estimate the relationship between different types of monitoring data and uncertain aspects of the species' natural history. Then, given the uncertainty remaining after POM, LEA was applied to assign conservation value to four alternative habitat allocations.

Results. Application of Decision Analysis for RCWs indicated that the best dispersal parameterizations derived from POM all agreed regarding which allocation of habitat would lead to the greatest number of LEA credits for the number of Potential Breeding Groups (i.e., abundance; PBG). However, the parameterizations disagreed regarding which habitat allocation would minimize habitat fragmentation effects, estimated as the departure of genetic variation farther away from a pre-settlement condition compared to that expected under the current recovery plan. Based on approximate costs associated with alternative habitat allocations, the cost-effective level of investment in future dispersal research, which may lead to a habitat allocation with greater conservation benefits at a lower cost, was estimated at \$1,036,679. Research in the Onslow Bight for RCWs also indicated that building landscape-scale models using less detailed RCW data from non-DoD partners did help to reduce uncertainty and improved management decisions for Encroachment Partnering (EP) programs.

Application of Decision Analysis to the GT indicated that the best emigration parameterizations derived from POM disagreed regarding which habitat allocation would provide the greatest conservation benefit for both abundance and genetic variation. Therefore, future habitat allocation decisions would benefit from either further model development and/or data collection. The habitat allocation that maximized abundance was different than the allocation that minimized the erosion of genetic variation; therefore, multiple services aide in habitat allocation decisions. Simulation results also indicated that GTs may be more sensitive to the fragmentation of habitat independent of the effects of habitat loss. Application of POM to develop and verify the IB-SEPM illustrated the relationship between model uncertainty and data commonly collected in the field. Results indicated that the mating system assumptions can have a large impact on the ability of the model to approximate data collected in the field. Extension of new techniques that integrate point pattern analysis with the landscape genetic data collected at FB indicated a mating system characterized by female philopatry and male biased dispersal. These genetic patterns, along with several demographic patterns collected in the field, indicated that strength of habitat preferences during dispersal for juvenile and subadult male dispersal also significantly impacted model fit. Certainly, much more work could be done to test the IB-SEPM, but this study has created a valuable framework with which to test hypotheses regarding GT natural history.

Benefits. By integrating POM & LEA, using Decision Analysis, the most cost-effective habitat allocation and/or translocation program can be identified given our existing knowledge about system dynamics. POM provides a method for constructing and verifying IB-SEPMs by including observed data that characterize the transient dynamics of the system. LEA provides a generally-applicable accounting system that allows for substitutions between habitat connectivity and area while maintaining equivalent ecological function at the landscape scale.

1.0 Objective

The Department of Defense (DoD) is increasingly engaging landowners outside installation boundaries to help protect biodiversity at a landscape scale. In practice, these efforts have resulted in cooperative purchase of parcels outside installations through the National Defense Authorization Act of 2003. The cooperative purchase of such properties to prevent residential or commercial development is referred to as the Encroachment Partnering (EP) program by the Marine Corps or as the Army's Compatible Use Buffer (ACUB) program by the Army. SERDP Exploratory Development (SEED) project (Bruggeman et al. 2007) evaluated how such habitat allocations would affect population viability for the red-cockaded woodpecker (*Picoides borealis*, RCW) on Camp Lejeune (CL). As an extension of that research, this project evaluated the contribution that different data types make to reducing uncertainty in individually-based, spatially explicit population models (IB-SEPMs), and, given this uncertainty, what is the most cost-effective allocation of habitat.

The broad objective of our research project is to address science questions in support of allocating habitat for at-risk species at broad geographic scales. Use of such polices requires estimates of how much change in landscape pattern can occur without decreasing population viability. To support the use of properties outside of installation boundaries to contribute to the persistence of at-risk species three objectives were addressed:

1. Evaluate the ability of lower quality monitoring data available outside military installations to reduce uncertainty in IB-SEPMs relative to the higher quality monitoring data available inside military installations. This objective was addressed using the RCW as a case-study organism because its natural history is relatively well-understood and a great diversity of monitoring data are available.
2. Evaluate the ability of Pattern Oriented Modeling (POM) and Landscape Equivalency Analysis (LEA) to estimate the conservation value of alternative landscape configurations, given uncertainty in dispersal. The strength and limitations of the approach were evaluated by contrasting landscape-scale results with patch-based results. Results for POM and LEA were integrated by applying Decision Analysis to IB-SEPMs using the Coastal North Carolina (NC) Recovery Population of RCWs as a case study. Decision Analysis provides a structured approach for including the influence of uncertainty when weighing alternative choices.
3. Evaluate the transferability of these approaches to lesser known species by evaluating alternative habitat allocations for the gopher tortoise (*Gopherus polyphemus*, GT) at Fort Benning (FB).

2.0 Background

Policies that permit the shifting of habitat for threatened, endangered, and at-risk species (TER-S) often must weigh tradeoffs among habitats at different locations and at different times. Both the spatial location and timing of land use change can affect the realized conservation benefit associated with any decision (Bruggeman and Jones 2008). The field of landscape ecology has not yet been able to provide a general theory useful for predicting the influence of landscape patterns on the occurrence and genetic structure of wildlife species (Lindenmayer and Fisher 2007; Bruggeman et al. 2010).

The influence of habitat arrangement, often discussed as habitat area and fragmentation, on biodiversity has engendered much debate (Fahrig 2003; Lindenmayer and Fischer 2007), making derivation of general rules needed for conservation planning difficult. Fahrig (2003) argued that when the influence of habitat fragmentation can be separated from the influence of habitat loss, as these structural (or geometric) changes are often confounded in real landscapes, the impact of fragmentation is much lower than habitat loss and can even have positive effects on biodiversity. The objective of Fahrig's review was to promote the idea that the effects of habitat loss and fragmentation across species can only be generalized when fragmentation is separated from the effects of loss – but no evidence to date supports this. On the contrary, researchers able to statistically control for the influence of habitat area and fragmentation separately have demonstrated that fragmentation can have a bigger, negative impact on biodiversity than habitat area and the response varies based on the amount of habitat and species' traits (Bruggeman et al. 2010; Hanski et al 2013).

The underlying problem with Fahrig's (2003) argument is that the populations are not impacted by habitat loss and fragmentation separately. Thus adequate consideration of the interaction of biological processes with landscape geometry was not included in Fahrig (2003), as the review was focused more on landscape ecology than population biology. Rates of recruitment and dispersal are often interconnected (Bruggeman and Jones 2008). As landscapes change, populations have no choice but to integrate effects of changes in habitat area and fragmentation as they attempt to reproduce and disperse. Even if separate theories for fragmentation and loss could be derived, as Fahrig et al. (2003) proposed, applying them in a management setting could be challenging.

Bruggeman et al. (2005) proposed a different solution, LEA, which avoided the debate created by the failure to recognize the interactions between population processes and landscape geometry, and recognized that such management challenges can benefit from applying economic incentives and that managers will often want to make tradeoffs between habitat area and connectivity. The objective of LEA is to provide a tradable credit system that moves the spatial allocation of habitat toward the habitat allocation in which the species evolved – thus helping to prevent the creation of conservation reliant species (Scott et al. 2010). LEA was derived using a combination of approaches in population biology, landscape genetics, and natural resource economics.

LEA starts by recognizing that species' traits have evolved to exploit scarce resources in a heterogeneous environment. As reviewed in Bruggeman et al. (2005), species in intact landscapes balance rates of recruitment and migration to prevent the expression of deleterious traits while maintaining genetic diversity within and among breeding groups. Fisher's Fundamental Theorem of Natural Selection states "the rate of increase in fitness of an organism at any time is equal to its genetic variance in fitness [variance in adaptive trait due to genetic component or 'adaptive genetic variance'] at that time" (Fisher 1930, pg 35). Because it remains difficult to identify and monitor components of genetic variance that underlie adaptive traits (Vernesi et al. 2008; Luikart et al. 2003), Moritz (2002) argues that the most effective means to protect adaptive genetic variance is to maintain viable populations across the mosaic of habitats in which they have historically been found (i.e., the context for selection), rather than the specific products of selection given past events.

While the immediacy of genetic threats to the viability of fragmented populations, relative to other threats such as environmental stochasticity, remains an area of scientific debate (Spielman et al. 2004), population genetic data provide a useful means for understanding how geometric changes in the landscape affect population processes (Manel 2003; Bruggeman et al. 2005; 2009). Further, recent research illustrated that genetic diversity is more sensitive to fragmentation than abundance (Bruggeman et al. 2010). Also, because habitat allocation decisions often require long time lags to establish the requisite vegetative characteristics and allow populations to achieve occupancy, the long-term impacts of habitat geometry on the evolutionary potential of the species should be considered. Thus, LEA includes population genetic theory to provide a tradable credit system designed to protect the environmental context that permitted adaptive evolution (i.e., maintaining historic rates of recruitment and migration across the landscape). LEA assigns greater conservation value to habitat allocations that move allele frequencies closer to that observed in a pre-settlement or unfragmented landscape where rates of inbreeding, drift, local extinction, and migration are maintained at levels associated with long term persistence. It does not matter if habitat allocations differ in habitat area or fragmentation, because LEA recognizes that rates of migration are often dependent on rates of recruitment and the goal is to maintain the environmental context for adaptive evolution (Bruggeman et al. 2005; 2009).

However, it is critical to have a good dynamic, spatially explicit population model that simulates interactions between changes in landscape pattern and population processes. The benefit of the IB-SEPM approach taken here is its focus on how biological mechanisms are affected by environmental heterogeneity, including patterns of land cover, rather than about debates regarding habitat loss versus fragmentation, which have not proven fruitful. IB-SEPMs have a proven ability to predict biological patterns in dynamic landscapes (Grimm 1999; Goss-Custard et al. 2006). IB-SEPMs are mechanistic models that simulate the explicit link between multiple biological processes (e.g., recruitment, migration, competition, and predation) and land cover patterns. IB-SEPMs, however, require a more detailed understanding of a species' natural history than analytical models historically used to seek generalizations about ecological processes. In fact, IB-SEPMs were initially criticized for containing large uncertainties due to the amount of data required to parameterize models of complex systems (Wennergren et al.

1995; Ruckelshaus et al. 1997; Beissinger and Westphal 1998). POM has been derived to construct and validate these models with less data than previously imagined (Grimm et al. 2005; Wiegand et al. 2004). POM accomplishes this by using additional information encoded in observed population-level patterns to reduce parameter error, providing a method for indirect parameter estimation.

This report illustrates how POM can be used to test hypotheses regarding how species traits interact with environmental heterogeneity for species regardless of how well understood they are. For the RCW, an IB-SEPM already exists thanks to 30 years of field studies on military installations. Despite tremendous knowledge of the species' mating system, there is still much uncertain regarding how the species disperses. Recent field efforts at Ft. Bragg (Moody et al. 2011) have used radio telemetry to track juvenile females, yet similar data are not available for males. Therefore, POM was used to test alternative dispersal hypotheses for males and females at a new location with the RCW IB-SEPM. For the GT, which is much less understood, POM was used to develop a new IB-SEPM at FB using as much demographic and genetic data as were available. Here, POM was extended to develop new techniques for building IB-SEPMs for such poorly studied species using population genetic data.

This report also illustrates how POM can be used to contrast the ability of alternative types of monitoring data to reduce uncertainty in IB-SEPMs. For the RCW, thanks to very mature monitoring programs conducted by independent agencies, POM was used to determine if the less detailed data collected outside of military installations could still be useful for learning about landscape-scale dynamics included in IB-SEPMs. Therefore, POM may become increasingly germane as DoD establishes partnerships with independent conservation organizations at broad spatial scales. In contrast for the GT, because such limited monitoring data were available, a smaller comparison of the utility of monitoring data was performed. However, for both species the extent to which different types of monitoring data provide redundant or complementary information for reducing uncertainty in landscape-scale dynamics for at-risk species is highlighted.

Decision Analysis (Clemen and Reilly 2001), a structured approach for contrasting alternative habitat allocations given uncertainty in system dynamics (e.g., dispersal and/or reproduction), was applied to both species by integrating LEA and POM. The most robust decisions under any policy are those able to achieve management objectives under a variety of possible states of nature (Hilborn and Ludwig 1993). By integrating POM & LEA, the most cost-effective habitat allocation and/or species relocation given our existing knowledge about system dynamics can be identified. This may provide a critical tool for DoD because military installations will often wish to change habitat allocations prior to reaching a scientific consensus regarding the natural history of at-risk species. The technique will allow managers to determine when it would be more cost-effective to forego changing habitat allocations and collect more monitoring data. Further, the opportunity costs of these management decisions are combined with existing levels of uncertainty regarding the influence of environmental heterogeneity on natural history traits to determine a cost-effective level of investment in research.

3.0 Contrasting the Ability of Monitoring Data to Reduce Uncertainty in RCW Dispersal using Pattern Oriented Modeling

POM was applied to evaluate the contribution different types of monitoring data make to reducing uncertainty regarding dispersal in the RCW IB-SEPM. Application of such uncertainty analysis is critical for DoD to be able to consider the influence of key uncertainties regarding the system being managed when evaluating the value of EP programs. The most robust decisions under any policy are those able to achieve management objectives under a variety of possible states of nature (Hilborn and Ludwig 1993).

The contribution that different data types make to understanding dispersal is largely unknown, because sites with multiple data sources are rare (Lowe and Allendorf 2010, Watts et al. 2007). Direct monitoring of dispersal through mark-recapture techniques or radio telemetry is common, but may be subject to bias due to small sample sizes (Finnegan et al. 2010) or limited spatial extent of study areas (Cooper et al. 2008). Population genetic techniques are often promoted as a more cost-effective approach for sampling large areas. The ability of population genetic data to provide indirect evidence of dispersal has long been debated (Nei 1986; Rousset 1997; Watts et al. 2007; Whitlock and McCauley 1999). In a few recent studies, dispersal was characterized using both radio telemetry and genetic data collected in the field, but these studies applied divergent statistical techniques suited to each data type (Cushman and Lewis 2010; Finnegan et al. 2010; Reding et al. 2013). Therefore, direct comparison of the ability of data types to estimate dispersal could not be made. IB-SEPMs provide a valuable tool for developing (Bruggeman et al. 2010) and evaluating (Lloyd et al. 2013) statistical methods in landscape ecology (Epperson et al. 2010).

Application of IB-SEPMs has led to conflicting views regarding the ability of genetic data to inform dispersal estimates. Cushman and Landguth (2010) concluded that genetic data are powerful proxies while Jaquiere et al. (2011) and Lloyd et al. (2013) concluded that genetic data provide weak signals of the influence landscape patterns have on dispersal. However, IB-SEPMs have not yet been used to contrast the ability of alternative data types (i.e., mark-recapture vs. genetics) to make inferences regarding dispersal.

IB-SEPMs were initially criticized for containing large uncertainties due to the amount of data required to parameterize models of complex systems (Wennergren et al. 1995; Ruckelshaus et al. 1997; Beissinger and Westphal 1998). However, POM has been derived to construct and validate these models with less data than previously imagined (Grimm et al. 2005; Wiegand et al. 2004). POM accomplishes this by using additional information encoded in observed population-level patterns to reduce parameter error, providing a method for indirect parameter estimation. Parameter error is the uncertainty associated with the parameter values used in a submodel. POM reduces parameter error in IB-SEPMs by removing parameterizations not capable of reproducing biological patterns observed in nature (Grimm et al. 2005). A pattern is defined as anything beyond random variation, or any signal beyond noise (Grimm et al. 1996).

IB-SEPMs have also been criticized because model complexity was perceived to limit rigorous model selection as is possible with information theoretical approaches applied to analytical models such as regression (Burnham and Anderson 2002). As illustrated in this study, recent approaches are now able to apply the principles of likelihood theory and information theory to parameterization and model selection in simulation models (e.g., Martinez et al. 2011; Wood 2010). The core of this approach is to reduce the observed data to summary statistics that capture the (dynamic) structure of the system (Matrinez et al. 2011; Wood 2010). Summary statistics represent the maximum amount of information in the simplest possible form (Csilléry et al. 2010) and should capture different characteristic features of the system that are relevant for the scientific question asked (Wiegand et al. 2004; Grimm et al. 2005). Use of multiple summary statistics is critical for model parameterization because multiple processes can generate the same pattern (e.g., both genetic drift and gene flow can change the degree of genetic distance among population units). The use of multiple summary statistics helps us identify which process is most likely responsible for the pattern observed (Grimm et al. 2005). The complexity of IB-SEPMs does provide the critical benefit of being able to simulate multiple patterns simultaneously.

IB-SEPMs are perhaps most productively viewed as experimental systems (Grimm and Railsback 2005). The present study adopts this approach to test the hypothesis that construction and validation of IB-SEPMs do not benefit from collecting data that vary in detail and spatial extent. To test this hypothesis, the ability of observed data, or summary statistics, that differ in spatial extent and level of detail to infer dispersal behaviors in RCWs was compared. Specifically, do different data sources provide new information regarding dispersal (i.e., the data are complementary) or do the data provide the same information (i.e., the data are redundant). If data at different spatial scales and levels of detail do not further limit parameter state space compared to parameter values observed when only data from CL are used, this would indicate that the data are redundant and do not help further reduce the prediction error of IB-SEPMs. If redundant data differ in cost of collection, then these results would help managers focus on the most cost-effective data sources. Monitoring data from across the Onslow Bight Landscape (Fig. 1), including CL, Holly Shelter State Game Lands (HS) and Croatan National Forest (CNF), were evaluated with POM to estimate the redundancy and complementarity of data sources.

Besides dispersal, the experimental framework provided by POM also permits the comparison of alternative reproduction models. The IB-SEPM was originally constructed at a site with bird banding data, and therefore good data on the age structure of the population, which was used to predict the number of fledglings (Letcher et al. 1998). However, many sites will not have data on age-structure or any demographic data at all. Remotely sensed data such as airborne laser altimetry (LiDAR) are becoming increasingly available, and here we assessed whether such data might provide a useful surrogate for demographic data allowing the estimation of fledglings per group. While high-density (>1 pulse/m²) discrete-return LiDAR (Maltamo et al. 2005) is more commonly used to relate forest structure to habitat quality for vertebrates (Bradbury et al. 2005), here we use low-density (<1 pulse/m²), discrete-return LiDAR, which was publically available. If a significant relationship between LiDAR-data and group size could be established, we proposed to use LiDAR-based group-size estimates to estimate expected

number of fledglings. Dr. Bruggeman served as a research associate briefly with Walters et al. (2011) and used the rich data source at Camp Lejeune to produce new reproduction submodels that included replacing age-structure data with only group size data to estimate the number of fledglings for a given breeding pair. The POM framework could then be extended to contrast the errors in predicted number of fledglings when demographic data were available or absent, thus rely only on LiDAR-based estimates of RCW productivity.

3.1 Methods

Details of the RCW IB-SEPM have been provided in Appendix A following the Overview, Design concepts, and Details (ODD) protocol, which is intended to provide a standard approach for describing agent-based models across studies to increase transparency (Grimm et al. 2010). The model was originally based on 15 years of bird banding data in the Sandhills Region of North Carolina (Letcher et al. 1998). The model simulates the cooperative breeding system of this species and tracks the fate of each bird in the population, which are assigned to one of four “classes” (breeder, helper, floater, or fledgling; Appendix A). The model has since been upgraded to integrate 23 years of bird banding data from CL. In updating the model, a new reproduction submodel has been derived to include the influence of both demography and climate on the number of fledglings produced each year (Appendix A). The updated model also includes a landscape classification for the Onslow Bight landscape that integrated information from the National Land Cover Database, LiDAR data collected by the Federal Emergency Management Agency in 2001, and ground collected forest metrics available on CL (Appendix A). The spatial extent of the landscape was approximately one million hectares and the grain was a one hectare cell (100 m x 100 m) (Fig. 1).

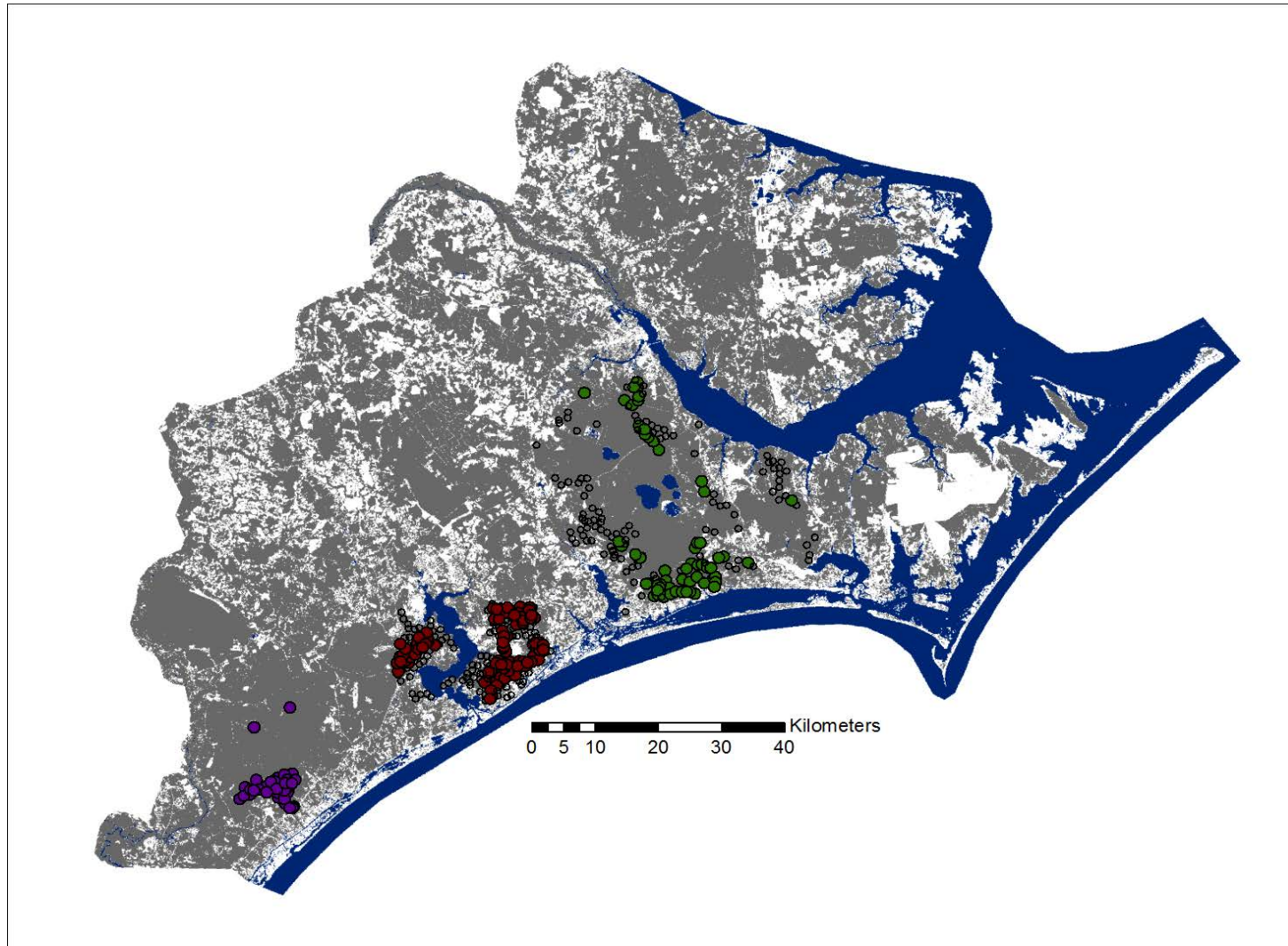


Figure 1. Distribution of RCW territories observed across the Onslow Bight in 2009. White areas are terrestrial gaps and blue are water gaps. Holly Shelter State Game Lands (HS), purple; Marine Corps Base Camp Lejeune (CL), red; Croatan National Forest (CNF), green.

The landscape was seeded using demographic data from each public landowner. As further described in Appendix A, Section 5, the simulation began with 48, 65, and 28 active territories in 1997 for CL, CNF, and HS, respectively. Territories were added or taken away each year as observed on each property from 1997 to 2009.

Population genetic summaries are included in the IB-SEPM to estimate the influence of genetic drift and gene flow at one hypothetical genetic locus that simulates an Infinite Alleles Model (IAM). Application of the IAM locus initializes the model without any gene correlations and allows spatial genetic structure to emerge over time from the influence of drift and gene flow (Bruggeman et al. 2009; 2010). The IAM locus was initialized by assuming founders to be heterozygous at the IAM locus and every founder was assigned two unique alleles (i.e., total alleles = 2 x number of breeders in the founding population). At CL a pedigree was derived from the bird banding data from 1986 to 1997. During this time all nestlings and adults were given unique color bands. All individuals not born on CL were treated as founders. The pedigree was then used in a gene drop. The gene drop simulates the transmission of alleles from parents to offspring assuming Mendelian inheritance (i.e., their offspring had an equal probability of inheriting each of the two alleles). Therefore, the initial population on CL begins POM with gene correlations that reflect mating events, and therefore relatedness of family groups and individuals, from 1986 to 1997. In contrast, it was assumed that all birds included in the initial population from HS and CNF were unrelated and were treated as founders. The expected apportionment of genetic variance within and among breeding groups was estimated by the method of Nei (1973), which was coded directly within the model.

3.1.1 Uncertain Parameters

Dispersal Uncertainty. A recent study of bird banding records in the Sandhills Region compared vegetative composition in used and unused dispersal paths between territories for males and females (Walters et al. 2011). A used path was defined as a path in which a helper or floater moved in a straight line between its present location and the location at which it became a breeder in a different territory. In contrast, an unused path was defined as a case in which a helper or floater was present but did not become a breeder where the vacancy existed. For males, no difference in vegetative composition between used and unused paths was found. In contrast, for females they found fewer non-forest gaps in used dispersal paths than unused dispersal paths. Females showed no avoidance of gaps less than 150 m, but rarely crossed gaps greater than 630 m. The probability of a female crossing gaps in between these sizes was estimated by:

$$P = 1 + \beta G$$

Where, β is a fitted coefficient (-0.00163 for females at Ft. Bragg) and G is gap length in meters. POM was used to evaluate the suitability of this approach for modeling floating behaviors in the Onslow Bight landscape within the RCW IB-SEPM. Further, POM allowed us to test new hypotheses, specifically, if water gaps affect dispersal behaviors, which is more germane in the Onslow Bight landscape than in the Sandhills. More specifically, this was accomplished by allowing β to vary independently, from 0 to -0.005, for water and terrestrial gaps for both males

and females. If the bird (male or female) encounters a gap (water and/or terrestrial), the dispersal model sums the size of water and terrestrial gaps. For each gap > 150 m and < 600 m, the equation above was used to estimate the probability of crossing the gap. If the gap is greater than 600 m then there was a 10% probability the bird would jump, or cross, the gap. Such jumping of large gaps has been observed during radio telemetry studies (Walters et al. 2011). When each bird encounters a gap the model draws a $u[0,1]$ random number and compares it to the probability of crossing the gap. If the random number is sufficiently small the bird will not cross the gap and turns 45 deg, either right or left chosen at random, to look for a new path. If the bird turns a full 360 deg without being able to move, the bird is left in its current location until the next season at which point it still may be able to compete for a breeding vacancy, may be able to move in the next season, or will die.

A terrestrial gap was defined as areas with roads, commercial or residential development, agriculture, or with vegetation height less than 7 feet (i.e., open areas and herbaceous wetlands, Table A1, Appendix A). Water gaps were identified using the National Landcover Database (Appendix A).

We also incorporated uncertainty regarding the number of steps taken by floaters each season, or “dispersal speed”. Previous estimates ranged from 2 to 5 km per year (Letcher et al. 1998). Therefore, this value was allowed to vary independently for male and female floaters from 100 m to 2 km per season (Table 1).

Competition Uncertainty. The original model (Letcher et al. 1998) assumed helpers and floaters could compete for breeding vacancies within 3 km of their current location regardless of intervening landcover types. The 3 km distance was defined as the bird’s perceptual distance, which is intended to simulate the bird’s foray distance. Given the observations of Walters et al. (2011), the model was updated to also include parameters to turn gap avoidance behaviors on or off during competition (Appendix A, Section 7) for breeding vacancies. If a gap greater than 150 m was present between a competitor’s current location and the breeding vacancy and gap avoidance behaviors were turned on, the individual was unable to compete for the vacancy. However, if gap avoidance was turned off, individuals could compete for any breeding vacancy within its foray distance regardless of gaps. Uncertainty regarding a bird’s foray distance was also incorporated. This value was varied from 1 to 60 cells, or 6 km, for helpers and floaters of both sexes, independently (Table 1).

Table 1. Model parameters estimated by inverse modeling for male and female individuals and their initial ranges. Cell size = 1 hectare, so 60 cells = 6 km.

Parameter	Range
Perceptual distance of helpers	1 to 60 [cells]
Perceptual distance of floaters	1 to 60 [cells]
Seasonal dispersal distance	1 to 20 [cells]
Strength of terrestrial gap avoidance (β_t)	0 to -0.005
Strength of water gap avoidance (β_w)	0 to -0.005
Sensitivity to terrestrial gaps during competition	0 or 1
Sensitivity to water gaps during competition	0 or 1

3.1.2 Summary Statistics

We reduced the raw observed data (patterns) into summary statistics that capture the observed population dynamics (Martinez et al 2011, Wiegand et al. 2004; Table 2). Each public landowner maintains an independent bird monitoring program. The detail, consistency, and time interval of data varied across landowners (see Appendix A, Section 6). CL provided the most detailed and consistent data, thanks to a bird banding program that has banded every nestling and adult since 1986. Five patterns were derived from these data (Table 2). PBG are defined as a breeding pair observed in the spring with or without nestlings or fledglings. Group size is the number of adult birds present in a territory including breeders and helpers of either sex. Connectivity was estimated for each sex separately, and is summarized as a matrix that enumerates the number of birds born in territory i that become a breeder in territory j from 1997 to 2009.

Two population genetic patterns were included from CL. Bird banding data were used to estimate a pedigree for all breeding events from 1986 to 2009, as described above. To derive the observed values for D_{ij} (Nei 1973) and number of unique allelic per breeding group A_i , the gene drop was iterated 10,000 times through the 888 breeding events observed. The mean and variance for D_{ij} and A_i in 2009 were also estimated.

The banding records for CNF were often incomplete. Therefore, detailed patterns such as connectivity or genetic diversity were not estimated. After discussions with current and former USFS staff, they questioned whether field monitoring was performed in a sufficiently consistent manner to include in POM. However, such issues may be common in other field sites and other species so these coarser patterns from 1997 to 2001 (i.e., PBG and group size) were included to test the sensitivity of our approach.

For HS, group size in 2009 was included as the only observed pattern. These data were collected by a supplementary field crew in 2009 because the historical nest check records did not consistently enumerate the adults at the nest.

Table 2. Description of observed data available from each landowner and their associated temporal and spatial scale.

Observed Pattern	Camp Lejeune (CL)	Croatan National Forest (CNF)	Holly Shelter (HS)
Potential Breeding Group (PBG)	1997 to 2009	1997 to 2001	NA
Group Size (Group)	1997 to 2009	1997 to 2001	2009
	Territories	Territories	Territories
	1 to 106	203 to 392	401 to 434
Connectivity (Conn)	Territories	NA	NA
	1 to 106		
Minimum pair wise genetic distance (D_{ij})	Territories	NA	NA
	1 to 106		
Unique Alleles per breeding group (A_i)	Territories	NA	NA
	1 to 106		

3.1.3 Estimates of Model Fit

In contrast to Bayesian model selection for statistical models, the high dimensionality, non-linearity, and stochasticity common to IB-SEPMs prevents direct estimation of the probability of the model given the data (Martinez et al. 2011). Approaches that can apply likelihood-based inference in complex stochastic simulation models have only been recently developed (e.g., Csilléry et al. 2010). One approach is to calculate the mean of multiple simulated runs to eliminate the internal model stochasticity, thereby treating the stochastic simulation model as deterministic on the level of the simulated summary statistics (Martínez et al. 2011). This approach was followed and likelihood functions $L[S|O]$ were estimated to describe the deviation between the summary statistics of the patterns observed in the Onslow Bight (O) and the patterns generated by each dispersal parameterization (S). Patterns generated by the IB-SEPM were collected in spring (Appendix A, Section 3) for the same time intervals and territories present in the observed patterns (Table 2). Averages for all simulated patterns were taken across the 200 Monte Carlo iterations for each dispersal parameterization. For count data, including PBG, group size, and connectivity, a Poisson negative log likelihood was estimated. For example, the negative log likelihood ($-\log[L]$) for group size on CL was estimated as:

$$-\log(L\{S|O\}) = \sum_{t=1997}^{2009} \sum_{i=1}^{106} -\log\left(\frac{S_{ti}^{O_{ti}} e^{-S_{ti}}}{O_{ti}!}\right)$$

Where t=year and i=territory. The temporal and spatial extent of data included in the $-\log[L]$ estimates for connectivity, PBG, and group size at other sites varied as described in Table 2.

For genetic data, in which the observed data were generated by a gene drop iterated 10,000 times, a Gaussian distribution was assumed.

$$-\log(L\{u^S|u^O, \sigma^O\}) = \sum_{i=1}^{106} \sum_{j=1, i \neq j}^{106} -\log\left[\frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(u_{ij}^O - u_{ij}^S)^2}{2\sigma^2}}\right]$$

Where, μ^S equals the average D_{ij} across 50 Monte Carlo iterations and μ^O and σ^O equal the mean and standard deviation for D_{ij} from the 10,000 iterations of the observed gene drop. The same approach was applied to number of unique alleles per breeding group on CL, except it was summed across the vector describing unique alleles per territory rather than a territory by territory matrix.

The goal is then to minimize the deviation between the summary statistics of the observed and simulated patterns; i.e., the parameterization must be determined that minimizes the negative likelihood functions.

3.1.4 Simulation Experiment

Alternative dispersal models were assembled from ranges for seven uncertain parameters used to simulate dispersal and competition (Table 1). Values from these ranges were sampled randomly with replacement using a Latin hypercube until 600,000 parameterizations were assembled. A systematic sample of the parameter space was required here because our aim was to compare the ability of different summary statistics to provide information for dispersal and competition. Each parameterization was iterated 200 times following standard Monte Carlo methods from 1997-2009. The deviation between patterns generated by each parameterization and patterns observed in the field (Table 2) was estimated as $-\log[L]$.

3.1.5 Pattern Redundancy and Complementarity

As an initial assessment of the potential data redundancy and complementarity among all the patterns, Spearman rank correlation coefficients were calculated in R 2.15 (`cor.test`), among the $-\log[L]$ values estimated for each summary statistic (or pattern) across the 600,000 parameterizations. If the $-\log[L]$ of two patterns were highly correlated, then the two patterns have a low deviation from the observations for the same parameterizations and large deviation for the same parameterizations. That means that the information contained in the two patterns is largely redundant. If the log likelihoods of two patterns were only weakly or not correlated the two patterns contain independent information. Finally, if the log likelihoods are negatively

correlated the information captured by the two patterns is conflicting. Note that our correlation assessment was conducted over the entire parameter space (i.e., 600,000 parameterizations). Therefore, only a few parameterizations may actually produce a good match and these parameterizations may not follow the overall correlation trend.

3.1.6 Filtering Parameterizations

From the initial 600,000 dispersal parameterizations tested, parameter state space was constrained by applying “filters”. By applying rejection filters, this demands simulated dispersal and competition parameters to closely approximate the observed summary statistics, as estimated by their associated $-\log[L]$ values. By including one or more summary statistics into a filter (Table 4), it provides a method for contrasting the ability of observed data to estimate dispersal parameters. For example, to contrast the ability of movement versus abundance data to estimate dispersal, parameters that result from applying filters A vs. B are compared (Table 4). To contrast the value of adding one year of abundance data from HS versus 13 years of abundance data from CL, filters B vs. C are compared; etc.

Filters were applied in two ways. First, to contrast the power of summary statistics, parameterizations were filtered by selecting only those with $-\log[L]$ values within the 0.05 percentile. Summary statistics that accept many parameterizations show low information content (i.e., weak patterns; Wiegand et al. 2003) because they are only able to weakly constrain the dispersal parameter space. In contrast, summary statistics that reject many parameterizations show high information content (Wiegand et al. 2003). Second, differences in parameter values that result by applying different summary statistics are contrasted. This was performed by adjusting the percentiles applied to the $-\log[L]$ -distributions for each filter (Table 5) to accept the ten best parameterizations.

3.1.7 LiDAR-based Estimates of Group Size

The State of North Carolina and the Federal Emergency Management Administration partnered to fund the collection of LiDAR data for the purpose of building high resolution digital elevation models for the entire state. LiDAR data were collected in the Onslow Bight from January to March 2001, with a sensor providing a nominal post spacing of 3 m and an average return density of 0.27 returns/m². These data were collected with sensors that yield a lower density of laser returns than is typical for forestry applications, nonetheless LiDAR data for the Onslow Bight contains 2.2 billion georeferenced three-dimensional points representing places where the laser pulses reflected off of vegetation, buildings, and the ground surface.

The software package Fusion/LDV (McGaughey 2009) was used to process the raw laser returns into forest structural information. Five LiDAR-derived metrics were used for the regression model: canopy height, canopy cover, midstory cover, understory cover, and total cover were calculated in an 800-m window around the territory center. A canopy height model was built using the Fusion tool “canopymodel”, which subtracts the return elevations from a model of the land surface and fits a smoothed spline surface to the tallest return. The Fusion tool “gridmetrics” was used to create raster estimates of total percent horizontal vegetation cover,

specifically canopy cover, midstory cover, and understory cover. Total vegetative cover was computed as the proportion of total returns greater than 0.61 m in height. Canopy cover was computed as the proportion of returns above 6.1 m in height. We defined midstory cover as the number of returns between 2.14 m and 6.10 m in height divided by the total number of returns below 6.10 m. Similarly, we defined understory cover as the number of returns between 0.61 m and 2.14 m in height divided by the number of returns below 2.14 m. Previous studies have shown that RCWs are particularly sensitive to mid-story structure between 2.14 m and the bottom of the forest canopy (Walters et al. 2002), so we selected height thresholds that were most applicable to RCWs. To examine how habitat heterogeneity influences group size, standard deviations for these variables were also calculated.

Mean group size on CL from 1998-2001 (n=64 territories) was found to be normally distributed and Ordinary Least Squares regression was applied to relate these values to a pool of habitat structural characteristics derived from LiDAR. To find the optimal model, we constructed all possible regression models.

3.2 Results

3.2.1 Pattern Redundancy and Complementarity

We find strong relationships between estimates of model fit for demographic and genetic data on CL, and weaker relationships between estimates of model fit for movement and genetic indices (Table 3). This suggests that both genetic indices are more strongly associated with the process of genetic drift than migration, because parameterizations able to replicate demographic patterns were also successful at replicating genetic patterns. The lower rank correlations associated with patterns describing movement suggests connectivity provides complementary information relative to all other data sources at CL. It also suggests that there is often movement that does not lead to reproduction. Stronger relationships between estimates of model fit for female connectivity and genetic variation were observed. Estimates of model fit for female connectivity were more strongly associated with patterns of allelic richness than genetic divergence. In other words, parameters able to closely approximate patterns of female connectivity were also able to approximate patterns of allelic richness. This suggests that allelic richness may be a stronger indicator of female movement than genetic divergence, which is perhaps not surprising because the mating system is characterized by female biased-dispersal that would result in new alleles being introduced to the breeding group thanks to longer-distance female movement. At the regional level, group size in 2009 at HS was moderately correlated with data from CL, also indicating some data complementarity. However, data for CNF report smaller correlation coefficients and were often negatively related to estimates of model fit from CL. While some data complementarity between CL and HS was observed, the relationship between estimates of model fit for these two sites was positive; thus, the same parameters led to a similar ability to approximate demographic patterns on CL and HS. In contrast, the negative relationship between CL PBG and CNF PBG indicates very different parameters are required to approximate demographic patterns at these two sites.

Such results confirm the suspicion that data from CNF contain greater observational error, so these estimates of model fit were not included into the filtering process described below.

Table 3. Spearman rank coefficients between $-\log[L]$ values that describe the goodness of fit for different summary statistics. Summary statistics available from CL include demographic patterns (Group: breeding group size, and PBG: number of PBG), movement patterns (M Conn: male connectivity, and F Conn: female connectivity), and genetic patterns (D_{ij} , and A_i : number of alleles in a breeding group). Data available from CNF included only PBG and breeding group size. HS included only breeding group size. $N=600,000$, $p<0.0001$ for all correlation coefficients.

	CL Group	CL M Conn	CL F Conn	CL D_{ij}	CL A_i	CNF PBG	CNF Group	HS Group
CL PBG	0.891	0.462	0.702	0.912	0.921	-0.156	0.0264	0.648
CL Group		0.550	0.637	0.928	0.927	-0.173	0.0891	0.719
CL M Conn			0.282	0.512	0.509	0.0906	0.514	0.756
CL F Conn				0.686	0.748	-0.0453	-0.0645	0.587
CL D_{ij}					0.990	-0.189	0.0562	0.708
CL A_i						-0.211	0.0447	0.714
CNF PBG							0.158	0.111
CNF Group								0.385

3.2.2 Filtering Parameterizations

First, parameterizations were filtered by selecting only those with $-\log[L]$ values within the 0.05 percentile of movement patterns (filter A), and reduced the parameterizations from 600,000 to 1,861 (Table 4). In contrast, application of the same percentile to demographic patterns from CL (filter B) left 5,955 parameterizations. Filter C included only group size data from 2009 at HS and left 29,987 parameterizations and is therefore a relatively weak pattern when used in isolation. The demographic and movement patterns from CL were combined into filter D and found 119 parameterizations. Adding HS patterns to movement and demographic patterns from CL (filter E) led to just one parameterization. When using only genetic distance patterns (D_{ij}), 30,005 parameterizations remained. Allelic richness patterns (A_i) were then added to D_{ij} patterns (filter G) to help control for drift and migration simultaneously, which reduced parameterizations to 16,113.

Table 4. Results from application of restriction filters at 0.05 percentile. The filters contrast the information content of different summary statistics collected at different levels of biological complexity and spatial scales.

Filter	A	B	C	D	E	F	G
					HS Group		
		CL Group	HS	CL Group	CL Group		
Summary		CL PBG	Group	CL PBG	CL PBG		CL D _{ij}
Statistic	CL Conn	CL PBG	Group	CL Conn	CL Conn	CL D _{ij}	CL A _i
accepted #							
parameters	1,861	5,995	29,987	119	1	30,005	13,892

Second, to contrast differences in parameter values generated by different summary statistics, the ten best parameterizations from filters A to G, described above, were accepted by adjusting the percentiles applied to the $-\log[L]$ distributions (Table 5). For filter A, a considerable reduction in uncertainty, as indicated by a narrow range of accepted parameter values, was observed for floater foray distance, dispersal speed, and terrestrial gap sensitive competition for both sexes (Table 5; Fig. 2). Therefore, a narrow range of values for these parameters is required to replicate connectivity patterns on CL. However, other parameters indicate a broader range of accepted values, indicating that either they are not critical for replicating movement patterns at the scale of CL or that they interact with other parameters.

When demographic patterns were used (filter B), uncertainty increased for dispersal speed and male floater foray distance, but it decreased for many parameters left uncertain by movement patterns, indicating that different processes contribute to replicating different patterns (Fig. 2). For example, female helper foray distance is effectively turned off by filter B, but was left uncertain by filter A. Female helpers only occur rarely in the field, but this result indicates that allowing female helpers to compete for breeding vacancies, as was observed under filter A, increases error in the demographic trajectory. The IB-SEPM assumes that female helpers have a higher survival rate than floaters, that competition favors older females, and middle-aged females produce more offspring (Appendix A). This shift in parameter values indicates that the processes associated with female helpers is likely still poorly understood, because permitting some female helpers to compete helps replicate movement patterns (filter A).

Similarly, strength of water gap avoidance for females shifts toward zero under filter B. However, under both filters A and C (i.e., only HS patterns) some avoidance of water gaps is indicated. Therefore, to replicate patterns of movement on CL and habitat occupancy on HS a reduction in movement due to water helps (Fig. 1), otherwise too many birds from eastern CL colonize western CL.

Uncertainty in female dispersal speed does decrease under filter C, indicating that the more scattered distribution of territories on HS necessitates longer dispersal. In contrast, female floater foray distance decreases indicating more restricted female forays help replicate patterns of habitat occupancy on HS, but male foray distances were similar to those observed under

filter A. Filter C indicates terrestrial gap sensitive competition is selected more often than observed in filters A and B, especially for males. Therefore, dispersal behaviors may be affected by local environmental differences not yet included in the IB-SEPM.

Filter D, which combines movement and demographic patterns from CL, provides very similar results to filters A and B. When demographic patterns from HS are added to these patterns from CL (filter E), increased uncertainty in female helper and floater foray distance and male terrestrial gap sensitive competition was observed. Therefore, to replicate patterns at regional scales a broader range of values are required for some parameters. Female dispersal speed, male floater foray distance, and female gap sensitive competition display consistent narrow ranges across filters A, C, D, and E; these parameters are critical for replicating observed patterns.

To determine the ability of genetic data to provide a surrogate for movement and demographic data, filter F included only estimates of genetic distance on CL (D_{ij}). Very similar parameter values were observed in most cases. The exception was dispersal speed for both sexes, which suggests that D_{ij} may not be sensitive enough to detect dispersal distance when applied using inverse modeling. Also certainty regarding water gap sensitive competition for females decreased, indicating more uncertainty regarding sensitivity of females to water gaps. Conversely, water gap sensitivity for males increased, indicating a reduction in uncertainty that males are sensitive to water gaps during competition. For female strength of water gap avoidance application of filter F moved the median estimate close to zero, but note under filter E the median value remained close to the median of the original range tested (Fig. 2). Under filter E results were more certain that water prevented competition for breeding vacancies (Table 5), but under filter F this was found to be more uncertain, indicating tradeoffs among female strength of water gap avoidance and water gap sensitive competition.

When patterns describing allelic richness were included with D_{ij} (filter G) uncertainty in parameter values decreased for female floater perceptual distance, dispersal speed, and strength of water gap avoidance. Interestingly, even with the inclusion of both genetic patterns uncertainty regarding male dispersal speed did not decrease, which suggests genetic data may not be sensitive enough to detect rare longer-distance movement of the philopatric sex.

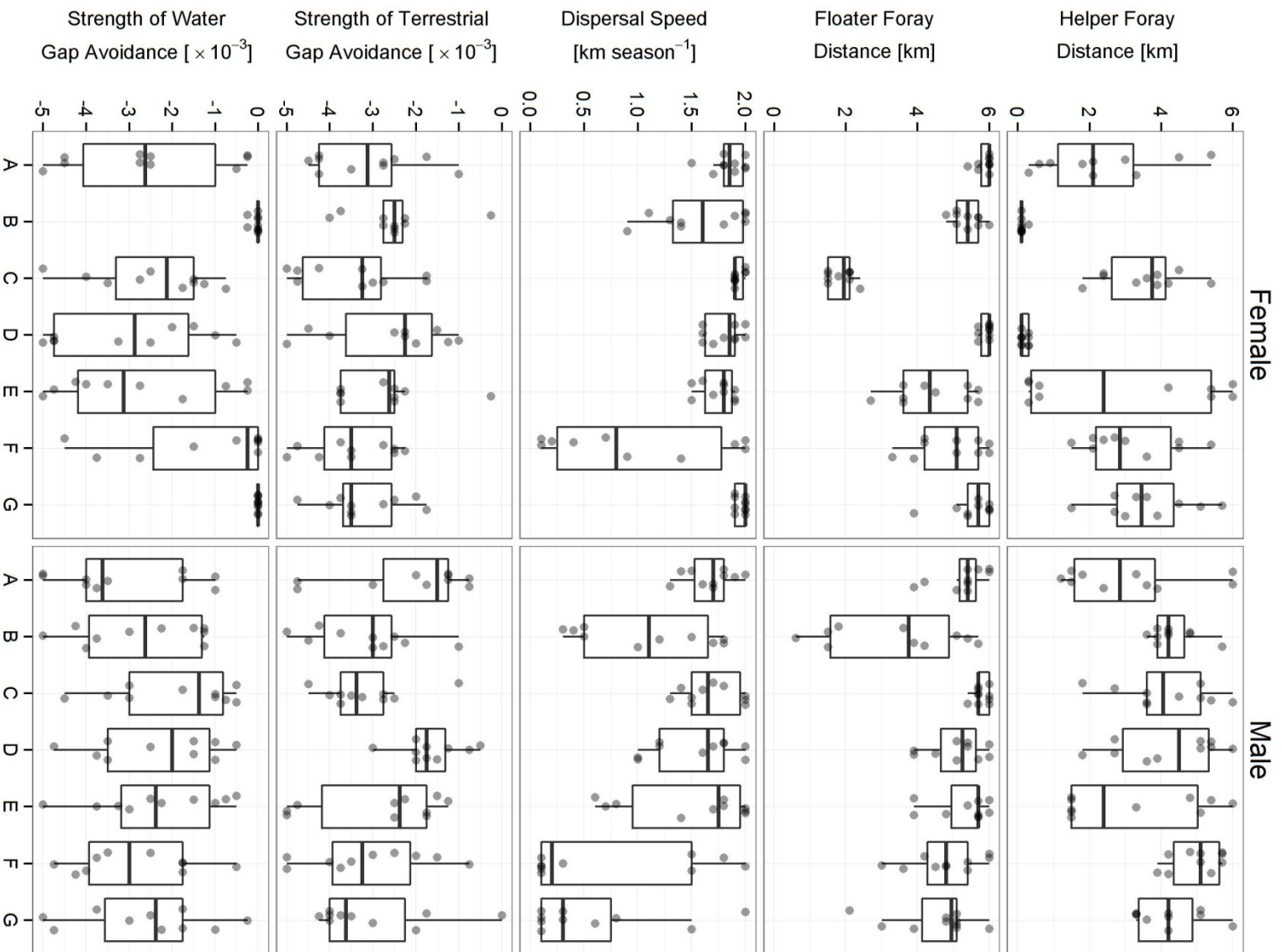


Figure 2. Parameter estimates for five of the seven uncertain parameters resulting from the application of filters A through G. Each filter accepts the ten best parameterizations able to approximate different combinations of summary statistics defined in Table 5.

Table 5. Results for sensitivity to terrestrial and water gaps during competition when the ten best parameterizations were accepted under each filter. These parameters were modeled as a binary variable. 1 = presence of a gap prevents a competitor from winning a breeding vacancy; 0 = gaps do not affect competition. Results presented as the average across the ten parameterizations (i.e., 0.5 = gap sensitivity turned off in half of accepted models).

Filter	A	B	C	D	E	F	G
		CL		CL	HS Group		
		Group	HS	Group	CL Group		
Summary	CL	CL PBG	Group	CL PBG	CL PBG		CL D _{ij}
Statistic	Conn			CL Conn	CL Conn	CL D _{ij}	CL A _i
Percentile	0.0037	0.0013	0.000015	0.021	0.0682	0.000015	0.00009
F Terrestrial	0	0	0.3	0	0	0.1	0.1
M Terrestrial	0	0.2	0.7	0	0.5	0.2	0.1
F Water	0.5	0.6	0.4	0.6	0.8	0.4	0.4
M Water	0.6	0.5	0.5	0.8	0.4	0.8	0.6

3.2.3 LiDAR-based estimates of group size

Habitat structural characteristics derived from LiDAR were not found to be related to mean group size on CL ($p > 0.1$, for all possible regression models). Therefore, we did not proceed with the comparison of reproduction models to contrast prediction errors when only remotely sensed data are available. Preliminary regression analysis detected a significant relationship when group size data from CNF ($n=79$) was included, thus more than doubling the sample size. However, given the observational error detected in the CNF data by the POM analysis (above), it is not appropriate to present these results.

3.3 Discussion

We used long-term movement, demographic, and genetic data of the RCW together with a detailed IB-SEPM to evaluate the ability of different data types to determine parameters and processes of dispersal. Different data types captured different aspects of dispersal. Mechanistic dispersal models (i.e., including forays, floating, and competition behaviors) able to generate results comparable to multiple types of empirical data are critical for understanding the underlying uncertainty associated with dispersal.

Application of our comparative statistical framework indicated that movement data were able to reduce uncertainty three-times more than demographic data (using a 0.05 percentile, filter A vs. B; Table 4). The comparative framework also highlighted the importance of data complementarity. While one-year of demographic data were useful on their own, they were most powerful when included with movement and demographic data collected at another site (0.05 percentile, filter D vs. E; Table 4). Thus matching movement and demographic patterns

simultaneously at regional scales was difficult. Movement data were the most powerful on their own (Table 4), especially critical for estimating foray distance and dispersal speed (Fig. 2). This result highlights the importance of maintaining long term bird banding programs on military installations. Abundance data on their own often led to likely erroneous parameter estimates (e.g., female helper foray distance and strength of water gap avoidance; Fig. 2). Therefore, forcing dispersal parameters to only approximate abundance, without simultaneously controlling for aspects of movement, can introduce bias toward parameters that have stronger impacts on population growth. Including demographic data, from both sites, and movement data did not always decrease range of parameter values able to replicate data collected in the field. On the contrary, these results illustrated that under filter E uncertainty in parameter values often increased (Table 5; Fig. 2). This result highlights that dispersal is indeed a stochastic process and that mechanistic dispersal models able to generate results comparable to multiple types of empirical data are critical for understanding the underlying uncertainty associated with dispersal (Bruggeman et al. in press).

When applying only genetic distance patterns (D_{ij}), derived from a 24-year pedigree, roughly the same number of parameterizations (0.05 percentile, filter F) resulted from only one year of demographic data (filter C; Table 4). Application of allelic richness patterns (A_i) and D_{ij} (filter G) removed an additional 13,892 parameterizations compared to filter F (Table 4). Therefore, in spite of the strong rank correlation between D_{ij} and A_i (Table 3), allelic richness still provided some complementary information. Using genetic distance as a summary statistic led to parameter values that were similar to that observed under filter E, except for dispersal speed for both sexes and strength of water avoidance for females (Fig. 2). Forcing to parameterizations to also approximate patterns of allelic richness corrected the problem for female dispersal speed (Fig. 2). Because A_i was slightly more correlated with PBG than D_{ij} , these results indicate that A_i and D_{ij} provide complementary information useful for replicating patterns of genetic drift and gene flow respectively.

We illustrated that basic census data are a more powerful predictor of dispersal than genetic data derived from a six-generation pedigree. However, results also indicated that when rejection filters were adjusted to accept the ten best parameterizations that genetic data can be very useful for estimating dispersal parameters in lieu of movement and demographic data; as one would expect based on population genetic theory (Nei 1986; Rousset 1997; Watts et al. 2007; Whitlock and McCauley 1999). Whether applying one IAM locus to a six-generation pedigree provides a weaker or stronger signature of genetic drift and gene flow than can be obtained by microsatellite loci isolated from tissues collected in the field is uncertain. One may argue that microsatellite data capture a longer history of landscape influences on dispersal. But separating recent from historic influences of landscapes change using microsatellite data can be difficult (Balkenhol et al. 2009). Also, the greater number of alleles included in the IAM locus compared to even many microsatellite loci may create stronger signatures of drift and gene flow. Ultimately, tissue samples from the field would be needed to test this. Granted, had genetic data been available at a larger geographic extent, genetic data may have been more powerful (Anderson et al. 2010). The application of the comparative statistical framework developed here is critical given the increasing use of genetic data to infer dispersal (Sork and

Waits 2010). The value of landscape genetic analysis can only be appreciated by contrasting the ability of genetic data to estimate landscape processes compared to other data types.

Inverse modeling techniques for IB-SEPMs based on summary statistics provide a useful framework for including new processes and observed patterns to learn how life history traits respond to environmental heterogeneity. Three key components allowed us to address uncertainty in dispersal in a rigorous manner. First, the model was initialized with as much observed data as possible which made comparisons to field observations possible (Appendix A). Second, stochastic components of reproduction, survival, and movement were allowed to interact. Third, information-theoretic approaches allowed us to contrast the contribution that different types of data make to revealing dispersal processes.

Though we were unable to detect a significant relationship between remotely sensed data and group size on CL, we feel the approach still has promise but likely requires a larger demographic sample size.

4.0 Application of Decision Analysis to Guide Habitat Allocations for RCWs across the Onslow Bight

Alternative allocations of habitat are often discussed based on geometric differences in the amount and spatial adjacency of habitat, commonly referred to as habitat area and connectivity, or conversely fragmentation. The extent to which species are affected by changes in habitat area versus connectivity will vary by species' natural history traits and landscape history (Bruggeman et al. 2005; 2009). Therefore, estimating how natural history traits such as dispersal are affected by alternative land cover classes and characterizing the initial state of the system, as detailed in the previous section, is critical. This also means that the field of landscape ecology has not yet been able to provide a general theory useful for predicting the influence of landscape patterns on the occurrence and genetic structure of wildlife species (Lindenmayer and Fisher 2007; Bruggeman et al. 2010). Therefore, estimates of changes in population structure due to landscape change required by LEA are made possible by using IB-SEPMs. Alternative habitat configurations are evaluated here using the reduced set of dispersal parameters identified with POM.

LEA is applied in this study to test the hypothesis that alternative landscape configurations provide the same level of function. This hypothesis is tested by contrasting abundance and genetic variation that result from alternative landscape configurations across the various dispersal models accepted by POM. Abundance and genetic variation are components of population structure that have direct significance for the viability of the species (USFWS 2003) and they differ in sensitivity to changes in habitat area and connectivity (Bruggeman et al. 2005; 2009; 2010). Ecological structure and function can be treated as goods and services when a direct or indirect benefit to humans can be demonstrated (deGroot et al 2002). This analysis assumes that the ecological services that provide these benefits are abundance and genetic variance (Loomis and White 1996; Bruggeman et al 2005). Because genetic variation is more sensitive to habitat fragmentation than abundance for RCWs (Bruggeman et al. 2010), it provides important information services (Fisher et al. 2009).

LEA is an extension of resource-based compensation applied to a landscape scale (Bruggeman et al 2005). Resource-based compensation determines the amount of restoration required to equate an individual's well-being before loss of an ecological resource with their well-being after that loss (Jones and Pease 1997). A "service-to-service" approach is used wherein adequate compensation is made to the public if the habitats restored provide equivalent types and levels of ecological services as the habitats lost. Application of LEA to naturally subdivided species such as RCWs estimates the equivalency of habitat patches traded in a fragmented landscape based on changes in three ecological services, 1) abundance and genetic variation 2) within and 3) among local populations, measured at the landscape scale.

Population genetic criteria are especially germane for RCWs because the recovery goal is based on the concept of variance effective population size (N_{ev}), which is defined as the size of an "ideal genetic population" (i.e, equal sex ratio, non-overlapping generations, etc.) experiencing the same rate of genetic drift as the study population (Kimura & Crow 1963). The N_{ev} is often

a fraction of the census population size (Frankham 1995a). Estimates of N_eV are critical for species of conservation concern as they indicate when drift will lead to the erosion of adaptive genetic variance (Palstra & Ruzzante 2008). The recovery goal for RCWs was based on the objective of maintaining a $N_eV = 500$ (USFWS 2003), a size believed large enough so that mutation offsets erosion of genetic variation due to drift and any deleterious mutations (i.e., genetic load) would be removed by natural selection.

N_eV is estimated based on the erosion of genetic variation at equilibrium, which creates a problem when attempting to compare alternative landscape configurations that will often differ in time required to reach equilibrium. LEA avoids this issue by simply contrasting erosion of genetic variation in non-equilibrium landscapes relative to a pre-settlement landscape. Recall, the pre-settlement landscape is assumed to represent the balance between rates of recruitment and migration in a subdivided population that minimize the expression of genetic load (Bruggeman et al. 2005; 2009). Therefore, the application of genetic variation within LEA to assign conservation value to alternative landscape configurations is intended to minimize the expression of genetic load while also providing information services regarding the change in balance between recruitment and migration (Bruggeman et al. 2005).

Changes in the balance between recruitment and migration will be reflected in rates of genetic drift, inbreeding, and local extinction. Bruggeman et al. (2009) used a simulation study to illustrate that these demographic-behavioral changes are captured by population genetic indices, average expected heterozygosity within breeding groups (H_S) and average genetic divergence among breeding groups (D_{ST}), which are based in Nei's (1973; 1977) theory of gene diversity in a subdivided population. Nei defines genetic diversity as the probability that any two alleles chosen at random are independent. H_S equals the probability that two alleles chosen at random from within an individual are independent, averaged across all breeding groups. D_{ST} reports the probability that two alleles are different when chosen at random from individuals in two different breeding groups (i.e., minimum genetic distance) averaged across the entire population. D_{ST} quantifies the extent to which the total population departs from random mating. D_{ST} would be zero if migration rates were high enough to approximate the random union of gametes at the total population scale, despite spatial subdivision of breeding groups. Bruggeman et al. (2009) showed that changes in H_S and D_{ST} capture the contribution that patches make to rates of recruitment and migration. In summary, H_S was primarily affected by drift and inbreeding while D_{ST} was primarily affected by migration and local extinction. In dynamic, spatially subdivided populations these biological processes are invariably linked. However, Bruggeman et al. (2009) showed that the proportional response of these indices will vary with the landscape context of the patches.

To illustrate how alternative habitat allocations can be compared including the effects of habitat loss and fragmentation and the influence of dispersal uncertainty, LEA and POM were integrated in this study using Decision Analysis (Clemen and Reilly 2001), a structured approach for including uncertainty in decisions,. A Decision Analysis case study was developed using the RCW to contrast the contribution EP parcels make to recovery of the RCW in the Onslow Bight landscape of coastal North Carolina. The Onslow Bight RCW population is already fragmented

across three public landowners: CL, HS, and CNF. The EP parcels considered differ greatly in habitat area, connectivity, and time of availability (i.e., forest maturity). This study illustrates how LEA and POM can be used to assign conservation value to these parcels and identify the most cost-effective habitat allocation that also minimizes habitat fragmentation.

4.1 Methods

4.1.1 Pattern Oriented Modeling

The five parameterizations able to provide the smallest $-\log[\text{Likelihoods}]$ simultaneously for demographic and connectivity summary statistics from CL and HS (i.e., Filter E as described in section 3.1.6) were used to evaluate alternative landscape treatments for LEA. To provide a comparison with knowledge of dispersal behaviors from Ft. Bragg, the dispersal parameters used in the RCW Decision Support System (DSS; Walters et al. 2011) were also applied.

4.1.2 LEA Simulations

LEA simulations were conducted from 2009 to 2108. Details regarding initial conditions, landscape data, model scheduling, and model parameters are provided in Appendix A. LEA compares results from alternative landscape treatments, including a Pre-settlement landscape (introduced above), a Recovery landscape, and Mitigation landscape. The Recovery landscape simulates the population as habitat is added to meet recovery goals for CL and CNF. The Recovery landscape describes the RCW population expected to result without addition of EP parcels. Then to generate one of many possible Mitigation landscapes, RCW territories are added on EP parcels to the Recovery landscape (see Appendix A [maps depicting these properties could not be included]).

4.1.2.1 Natural Colonization vs. Translocation

The time at which a territory becomes available on an EP parcels, based on habitat evaluations, directly affects its conservation value (Bruggeman and Jones 2008). Therefore, the simulations are temporally explicit, and this level of detail leads to two management options. The first approach is “Natural Colonization”. Under Natural Colonization, territories are added if the habitat is suitable by year t , and there are at least 6 territories that can be made available for RCWs by the year t that are within 3.2 km of a another possible available cluster with another nearest neighbor within 3.2 km, which may or may not be already occupied by RCWs. Territories meeting these spatial criteria are “connected components” of an EP parcel. If a connected component contains a minimum of six territories, all EP territories will be included in the simulation and may be found by floaters or helpers seeking a breeding vacancy. Also, more than one connected component can be found on EP parcels and made available for RCWs.

The other approach is “Translocation”. Translocation also begins by identifying connected components. But in this case, connected components are limited to six territories and if more than one connected component is found, the connected component that is adjacent to the largest number of active territories is selected for translocation. Then three female fledglings

are selected at random, from no less than 2 territories, and three male fledglings are selected at random, from no less than 3 territories that contain at least one helper, from CL in the fall season. The males and females are moved as pairs to randomly selected territories in the connected components. These birds are classified as floaters and compete for breeding vacancies as described in Appendix A. Importantly, if floaters are in the area due to simulated dispersal processes (i.e., and not translocation), these translocated birds would then have to compete with floaters for the vacancies. To simulate the lower success of translocated birds observed in the Southern Range Translocation Cooperative during 2007-2010 at 50 different properties (McDearman 2011), seasonal probability of survival for translocated birds that become breeders was adjusted from 0.95 to 0.63.

4.1.2.2 Environmental stochasticity

The influence of environmental stochasticity on reproduction was included using a new submodel that includes the influence of seasonal weather data on reproductive success (Appendix A, Section 7). For these simulations, weather data for the years 2010-2108 was estimated by randomly sampling distribution for temperature and wind from New River Marine Corps Air Station weather station and precipitation data from the weather station at Hoffman Forest. No trend indicative of climate change was detected in these data, which only dated to 1996, so no climate changes scenarios have been included in the present study.

4.1.2.3 Genetics

All birds were assigned alleles at five hypothetical genetic loci. The first allele assumes that every founding individual is heterozygous and contains two unique alleles (i.e., total alleles = 2 x number of breeders in the founding population, an IAM of genetic variation). Therefore, by definition offspring that inherit the same allele from both parents, assuming Mendelian inheritance including independent segregation, are identical by descent allowing a direct estimate of Wright's inbreeding coefficient (Bruggeman et al. 2009; 2010). The IAM locus also allows us to initialize the simulation without any positive spatial autocorrelation in genetic data. Therefore any spatial genetic structure that results over the course of the simulation is due to patterns of migration, drift, inbreeding, and local extinction.

In addition, four more loci with lower levels of allelic richness to parallel levels of genetic diversity observed in nature were added. Using tissue samples from 28 birds at Avon Park Air Force Range, Fike et al. (2009) characterized 25 polymorphic microsatellite loci and found that the number of alleles per loci in RCWs ranged from five to two, so four loci that sampled alleles from a normal distribution with standard deviations including 1.0, 0.5, 0.25, and 0.05 were included to approximate observed levels of allelic richness. However, for these four loci genetic correlations across the landscape reflect the simulation initialization procedure. For example, levels of relatedness between birds on HS and CNF would be high because their alleles were generated by sampling the same distribution, and this correlation could not be viewed as a signature of dispersal. These loci were included simply to provide an estimate of how many alleles might be present at a local scale (i.e., a territory) in the field.

We assumed one migrant per generation (OMPG) was introduced into the landscape at a randomly selected territory on CL, HS, or CNF. This migrant was assumed to be unrelated to the existing population at the IAM locus, and was introduced as a floater. Therefore, it was left uncertain whether they actually bred and introduced the new alleles to the population. It is important to note the OMPG assumption was also included in the POM modeling (Appendix A).

Details of the population genetic metrics have been summarized elsewhere (Appendix A; Bruggeman et al. 2009; 2010). The expected apportionment of genetic variance within and among breeding groups was estimated by the method of Nei (1973) for the IAM locus. Nei's theory relates the total genetic diversity in the population (H_T) to the average genetic diversity within breeding groups (H_S) and average genetic divergence among breeding groups (D_{ST}), $H_T = H_S + D_{ST}$. Due to the monogamous mating system, breeding groups were treated as the "subpopulation" because they represent the spatial scale at which alleles are combining at random (Sugg et al. 1996). Under an IAM Wright's inbreeding coefficient, the probability that two alleles chosen at random from within a breeding group are identical by descent, was estimated as: $F = 1 - H_O$ (Miller & Lacy 2005), where H_O equals the average observed frequency of heterozygous individuals within a breeding group. F_{ST} was also estimated (Nei 1977), which equals the proportion of total genetic variation due to population subdivision. F_{ST} is estimated as $F_{ST} = 1 - H_S / H_T$, and is negatively related to migration rates among breeding groups. F_{ST} was not used to evaluate equivalency of habitat allocations because it is a proportional measure that may fail to detect important changes in ecological function. For example, two alternative landscapes may have the same F_{ST} values but have very different values for H_T , which may result due to differences in rates of local extinction. Similarly, alternative habitat allocations are not compared using Wright's inbreeding coefficient as it only characterizes one process, inbreeding. By contrasting H_S and D_{ST} separately across alternative landscape configurations the influence of genetic drift, inbreeding, migration and local extinction can be evaluated (Bruggeman et al. 2009). Variance NeV (Appendix A) was also estimated.

4.1.2.4 LEA Accounting

LEA estimates the conservation value of alternative landscape configurations by including both demographic and genetic criteria. LEA incorporates a "spatially-explicit" planning objective as the allocation of habitat yielding the spatial apportionment of neutral genetic variance observed prior to habitat loss and fragmentation (i.e., a pre-settlement landscape) (Meffe 1996; Bruggeman et al 2005). The Pre-settlement landscape (Appendix A) represents the spatial distribution of habitat in which rates of recruitment and migration achieve this balance. The conservation value of a LEA credit increases as habitat allocation decisions move the balance between rates of recruitment and migration closer to levels observed in a "Pre-settlement" apportionment of habitat. This reduces the probability that changes in recruitment and migration would lead to the expression of deleterious traits that result from mating between close relatives (inbreeding depression). Similarly, this reduces the probability that changes in migration would disrupt locally adapted gene complexes due to mating between individuals from different regions (outbreeding depression). In this way, LEA focuses on protecting the environmental context that permitted adaptive evolution, rather than attempting to identify all adaptive components of genetic variance (Moritz 2002).

LEA estimates credits and debits associated with landscape change as Landscape Service Years (LSY; Bruggeman et al. 2005), which is a time-integrated estimate of the proportional change in ecological services relative to the sustainability goal due to marginal change in landscape structure. The expected number of abundance credits is estimated as LSY - Abundance (LSY_C^N):

$$E[LSY_C^{PBG}] = \sum_{t=W}^{100} \left(\frac{m_t^{PBG} - r_t^{PBG}}{r_t^{PBG}} \right)$$

where W is the time territories on EP parcels are added, r_t^{PBG} is the expected total abundance in breeding groups at year t provided by the Recovery landscape, and m_t^{PBG} is the expected total abundance in breeding groups at year t provided by the Mitigation landscape.

Calculating credits associated with changes in genetic variance is more complex. The management goal is to approximate population services provided by the distribution of habitat in which the organism evolved (Meffe 1996). Greater genetic diversity within a breeding group or greater genetic divergence among breeding groups is not always better for sustainability (Bouzat 2001). The levels of genetic service provided by the baseline landscape will be used to direct trading toward this goal. As estimates of genetic variance within and among breeding groups move closer to baseline levels due to restoring habitat area or connectivity, the more credit is accrued in the bank. The credit representing a marginal change in genetic services associated with the mitigation landscape can be calculated as LSY - Genetic Variance (LSY_C^G):

$$E[LSY_C^G] = \sum_{t=W}^{100} \left(\frac{|b_t^G - r_t^G|}{b_t^G} \right) - \sum_{t=W}^{100} \left(\frac{|b_t^G - m_t^G|}{b_t^G} \right)$$

where G is the genetic variance component estimated (H_S , D_{ST} , or H_T), b_t^G is the expected level of genetic variance at year t provided by the Pre-settlement landscape, r_t^G is the expected level of genetic variance at year t provided by the Recovery landscape, and m_t^G is the expected level of genetic variance at year t provided by the Mitigation landscape. The first summation reports the extent of habitat fragmentation present in the Recovery landscape prior to mitigation. The second summation, to the right of the minus sign, reports the level of fragmentation after RCW territories are made available on EP parcels. LSY_C^G then equals the degree to which EP parcels reverse the effects of fragmentation.

4.1.2.5 Random Permutation Testing

We use 200 Monte Carlo simulations to estimate distributions describing the expected influence of alternative landscape configurations on ecological structure and function. Therefore, this report focuses on presenting median and mean expectations generated from the IB-SEPM. Additionally, the null hypothesis that any differences in distributions generated from alternative model assumptions (e.g., with and without EP parcels, or Recovery vs. Mitigation landscapes) result due to chance was tested by employing random permutation testing (Manly 1986). Accepting the null hypothesis means that the two distributions are equally likely despite the addition of new habitat, for example. The p-values presented are then inversely related to the strength of evidence against the null hypothesis.

Random permutation testing was applied at two spatial scales. The first was the landscape scale. Here, the distribution of PBG, H_S , D_{ST} , and H_T observed at year 100 across the 200 Monte Carlo iterations in the two landscape treatments were compared (i.e., Recovery and Mitigation). A distribution of randomly generated median differences was generated by pooling the 200 iterations across landscape treatments and estimating “random” medians by taking two random samples, ignoring treatment labels, of 200 results, 10,000 times. The distribution of random medians was then used to estimate the probability of observing the median difference between landscape treatments if the difference were due to chance.

The second spatial scale was the patch or territory scale. For all patches except those on an EP parcel (i.e., mitigation territory), random permutation testing was used to determine if the attribute (Table 6) mean changed significantly due to addition of habitat on the EP parcels. Again, a random distribution of mean differences ($n=10,000$) was generated by sampling from the 200 iterations for each patch. The difference in attribute value for a patch in a landscape with and without EP parcels may be negative or positive, so p-values are reported designating whether they relate to a negative or positive effect size.

Table 6. Summary of attributes used to describe patch- (or territory-) level changes.

Attribute	Description
Alleles	Number of unique alleles at locus 2 (sd = 1.0) at year 100.
Extinction	Probability of local extinction averaged over the number of years the patch was available for occupancy
F_immigration	Total number of female migrants received by a patch
Group	Group size (number of breeders and helpers) averaged over the number of years the patch was available for occupancy
Inbreeding	Wright’s Inbreeding coefficient at year 100
M_immigration	Total number of male migrants received by a patch

4.2 Results and Discussion

4.2.1 Recovery Landscape

In order to estimate landscape function assuming no addition of EP parcels across the Onslow Bight (i.e., no landscape change), a variety of landscape-scale metrics were evaluated (Table 7). The median expected value for PBG exceeded the census population goal of 350 PBG for all parameterizations selected from POM (Table 7). However, expected PBG from the DSS dispersal parameterizations was 347. The ratio of effective to census population size varied across dispersal parameters but was consistently lower than reported by Reed et al. (1993; $N_e:N_c = 0.65-0.8$), which served as the basis of the recovery goal (USFWS 2003). Therefore, the application of existing recovery plans is not expected to meet the recovery goal of $N_eV=500$, and erosion of adaptive genetic variation due to drift may be a concern. Importantly, average rates of inbreeding after 100 years remained below 0.125, the threshold at which inbreeding

depression has been observed in the Sandhills (Daniels and Walters 2000). Though, it is important to recall that the simulation assumes all breeders are unrelated at the start of the simulation. Initializing the simulation with estimates of observed levels of inbreeding would better help assess the ability of Onslow Bight Recovery population to avoid inbreeding depression.

The lowest rates of inbreeding, lowest F_{ST} , and highest NeV was observed for POM 3 (parameter values are reported in Table A5). These genetic results all indicate higher migration rates and lower rates of genetic drift under POM 3, which is characterized as the only parameterization with female water gap sensitive competition turned off, the largest value for male helper foray distance, and the lowest avoidance of water gaps by male floaters among parameters selected with POM. Among the POM parameters, the highest inbreeding and F_{ST} values were observed for POM 2, which is characterized by having female water gap sensitive competition turned on, small foray distance for male floater, and the strongest water gap avoidance for male floaters among the POM parameters. The highest rate of inbreeding and F_{ST} was observed for the DSS parameters, while NeV provided an intermediate value for this parameterization. Therefore, rates of drift are not higher than observed under the POM parameters, perhaps due to less restrictions on male movement included in the DSS compared to the POM parameters (Table A5). However, fragmentation effects, expressed through inbreeding and F_{ST} , are indicative of lower rates of female dispersal, as indicated by lower female floater dispersal speed and female foray distance, compared to POM parameters (Table A5).

Table 7. Median values expected at year 100 in the Recovery simulation.

	POM 1	POM 2	POM 3	POM 4	POM 5	DSS
F	0.081	0.092	0.076	0.087	0.085	0.102
F_{ST}	0.298	0.303	0.295	0.300	0.301	0.313
NeV	225	230	331	278	254	245
PBG	367	366	367	370	372	347
¹ NeV:Nc	0.306	0.314	0.451	0.376	0.342	0.352

¹Nc = 2*PBG

4.2.2 Mitigation Landscape: Shaken Creek

The equivalency of landscape function for each possible Mitigation landscape relative to the Recovery landscape was estimated comparing PBG, H_S , D_{ST} , and H_T over time applying the LEA equations. Results for each property are include in Appendix B, but here only results for Shaken Creek are provided as they provided the best way to understand how LEA can be used to capture conservation values under different management choices.

When examining the proportional change in population growth that results from adding RCW habitat on Shaken Creek, estimated here as credits for PBG (LSY^{PBG}), an increase in abundance over time was observed (Table 8; Fig. 3). Random permutation testing indicated a statistically significant difference in PBG observed at year 100 between the Recovery and Mitigation landscapes for all parameterizations ($p < 0.05$). For most parameterizations translocating birds

increased the number of abundance credits compared to natural colonization, but not always. POM 2 and 5 indicated a smaller credit when translocating compared to natural colonization, and the biggest benefit of translocation was observed for the DSS parameterization.

Table 8. Conservation value of adding habitat on Shaken Creek expressed as Landscape Service Years (LSY) for each ecological service. Results are presented for the five best parameterization identified using POM and the DSS parameterization assuming natural colonization (NC) and translocating birds from CL (T). Values in bold were statistically significant based on random permutation testing ($p < 0.05$).

	LSY PBG	LSY H_S	LSY D_{ST}	LSY H_T
POM1 NC	2.58	-0.0562	-0.203	0.0134
POM1 T	2.71	-0.105	-0.343	0.0134
POM2 NC	3.08	-0.172	-0.560	0.0215
POM2 T	2.89	-0.0781	-0.327	0.0283
POM3 NC	2.54	-0.0134	-0.176	0.0385
POM3 T	2.63	-0.0586	-0.259	0.0224
POM4 NC	2.27	0.0448	-0.00916	0.0337
POM4 T	2.39	-0.0497	-0.211	0.0215
POM5 NC	2.73	-0.0140	-0.142	0.0272
POM5 T	2.63	0.0641	0.0157	0.0386
DSS NC	2.07	-0.236	-0.696	0.0127
DSS T	3.18	-0.346	-0.956	0.00340

Assuming natural colonization, credits for H_S were less than zero for most parameterizations, suggesting that the addition of Shaken Creek increased rates of genetic drift and inbreeding averaged across the landscape. However, none of the parameterizations resulted in a statistically significant difference between H_S observed at year 100 between the Recovery and Mitigation landscapes ($p > 0.05$; Table 8). Property-specific distributions indicate rates of immigration and group size on Shaken Creek are consistently smaller than CL or HS (Figs. B8, B10, B11). Inbreeding and F_{ST} approximated values observed in the Recovery landscape (Table B2) but were not used in the LEA calculations to contrast habitat allocations as discussed in the Methods.

Assuming translocation of birds, credits for H_S were less than zero for most parameterizations (Table 8). Compared to natural colonization, erosion of genetic variation within breeding groups tended to increase for POM 1, 3, 4, and DSS parameterizations (Fig. 3). Statistically significant differences between Mitigation and Recovery levels of H_S were only observed with POM 1 and DSS. Examining property specific distributions with and without translocation indicates that translocation improves ecological function on Shaken Creek to a certain extent (i.e., more immigrants, more alleles, and bigger group size; Appendix B, Figs. B19-B30). However, examination of patch-based statistics indicates that for POM 1 a greater number of patches on CL, HS, and/or CNF have a greater rate of inbreeding relative to a landscape without Shaken Creek (Appendix B, Fig. B4). Similarly for the DSS a greater number of patches on CL,

HS, and/or CNF have fewer unique alleles. Therefore, the statistically significant negative credits observed for POM 1 and DSS, assuming translocation, likely result from increased inbreeding under POM 1 and increased drift under DSS. Among the POM parameters, POM1 had similar low dispersal speed for female floaters as observed under DSS, and assumed a relatively strong impact of water on dispersal behaviors (i.e., water gap sensitive competition was turned on and strength of water gap avoidance = -0.00425; Appendix A, Table A5). In contrast, as previously discussed, the DSS assumes shorter dispersal and foray distances for males compared to POM parameters. The majority of translocations occurred for POM1 and DSS parameterizations (Table 9). **Therefore, LEA detected translocations reducing genetic variation in the source population.**

Assuming natural colonization, credits for D_{ST} were less than zero for all cases, but only statistically significant for POM 2 and DSS parameterizations. Comparison of patch distributions for Shaken Creek, CL, and HS (Appendix B, Fig. B19) indicate greater probability of local extinction was observed on Shaken Creek for POM 2 and DSS compared to other parameterizations. Local extinction is a stochastic process that may contribute to increased genetic divergence among breeding groups (Barton & Whitlock 2004).

Assuming translocation, credits for D_{ST} were less than zero for all parameterizations except POM 5 (Table 8). Translocation increased genetic differences among groups, compared to natural colonization, for POM 1, 3, 4, and DSS parameterizations (e.g., Fig. 3), but only statistically significant for POM 1, 3, and DSS. Comparison of patch distributions for Shaken Creek, CL, and HS (Appendix B, Fig. B25) indicate greater probability of local extinction was observed on Shaken Creek for POM 1, 3 and DSS compared to other parameterizations, and especially compared to natural colonization.

For both natural colonization and translocation, credits for H_T were greater than zero for all parameterizations and statistically significant for all except POM 2. Therefore, the addition of Shaken Creek is expected to help retain more genetic variation at the total population level. However, as summarized above this results due to retaining more genetic variation among breeding groups rather than within breeding groups.

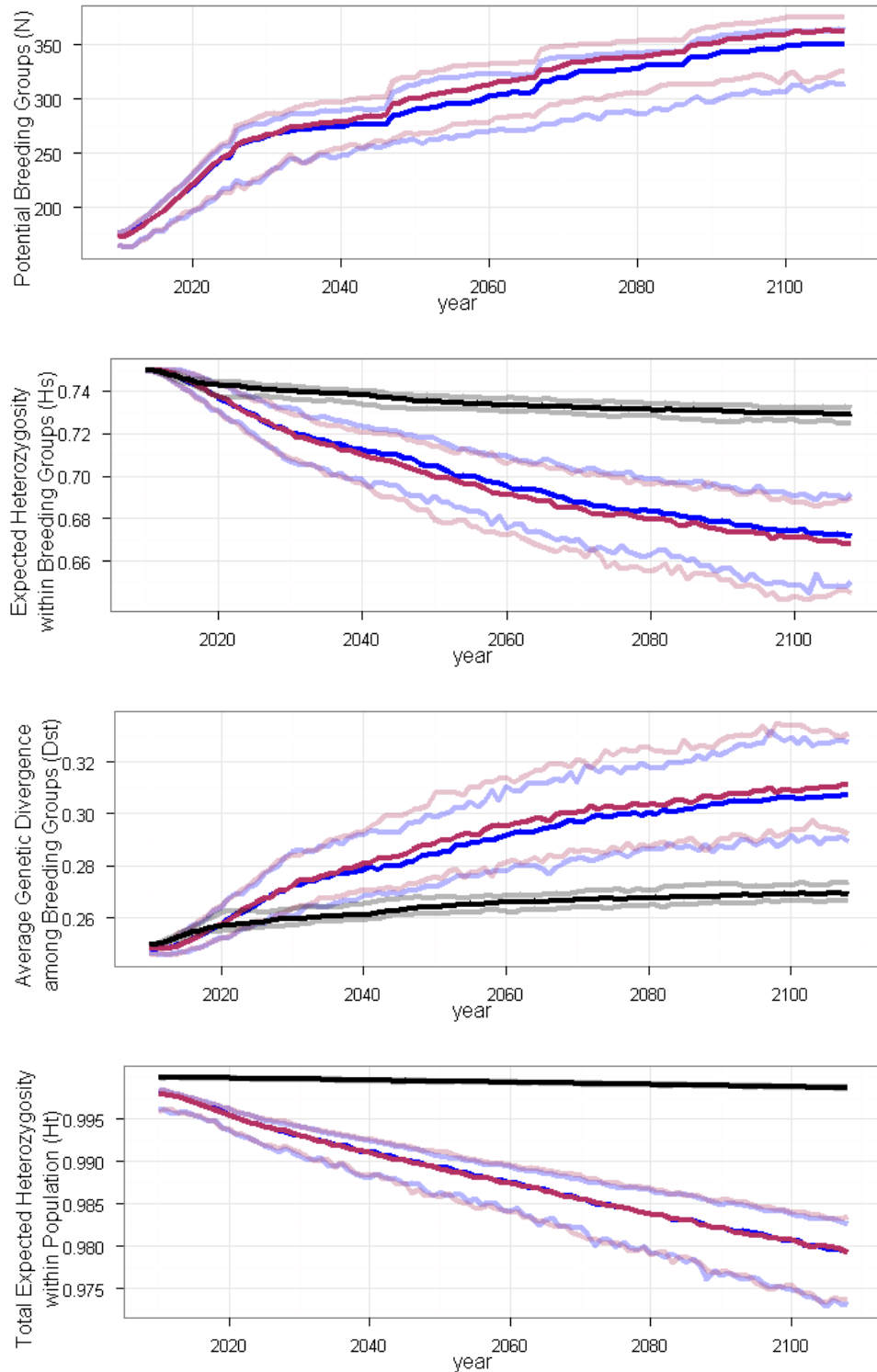


Figure 3. Median and 95th percentile values (n=200 Monte Carlo iterations) for ecological services included in LEA for the DSS parameterization assuming translocations. Black, Pre-settlement landscape; Blue, Recovery landscape; Red, Mitigation Landscape (i.e., addition of Shaken Creek).

Table 9. Average number of pairs translocated. Average was taken across 200 Monte Carlo iterations.

	POM1	POM2	POM3	POM4	POM5	DSS
Bear Garden	50.7	47.1	52.0	45.9	44.1	99.8
Shaken Creek	19.2	12.1	10.4	11.2	13.7	29.8

4.2.3 Making Cost-effective Decisions under Uncertainty

4.2.3.1 Decision Analysis

Across all possible Mitigation landscapes considered and dispersal parameterizations (Appendix A, Table A5), our results report a range of possible effects that changing habitat area and connectivity might have on RCWs across the Onslow Bight (Appendix B, Table B1). Decision Analysis was used to reduce the dimensionality of the results in Table B1 so that the role of uncertainty could be more formally incorporated into habitat allocation choices (Raiffa and Schlaifer 1961; Clemen and Reilly 2001). Choices were ranked based on the number of LSY credits for each of the four ecological services. Number of LSY remaining is a time-integrated estimate of the net gain or loss of ecological services due to the change in landscape structure. The most simple way to reduce the dimensionality of results is to calculate the Expected Value (EV) of a choice given uncertainty in dispersal behaviors captured by the five parameterizations [or models] selected by POM is estimated as:

$$EV[Choice|Model] = \sum_{Model=1}^5 P[Model] * LSY_{Model,Choice}$$

Where, Model is the index for the five uncertain parameterizations, $P[Model]$ is the prior probability that a parameterization is true, $LSY_{Model,Trade}$ is the number of LSY credits generated by the addition an EP parcel under a model, as reported in Table B1. All five models were able to reproduce demographic and connectivity patterns, therefore, we that each model was assumed to have an equal probability of being true, $P[Model]=0.2$. The choice with the greatest expected value is referred to as the preferred choice ($EV[Choice_p|Model]$).

For PBG the preferred choice, given uncertainty in dispersal behaviors, is to introduce habitat on Oak Island and southern Greater Sandy Run Area (Table 10). In contrast, for H_S the preferred choice is to introduce habitat on Bear Garden and implement a translocation program. For D_{ST} the preferred choice is to introduce habitat only on Oak Island, and for H_T it is to add habitat on Bear Garden without translocation. However, LSY for H_S and D_{ST} indicate an increase in rates of drift, inbreeding, and extinction within breeding groups and a decrease in rates of migration among breeding groups (i.e., negative LSY values are reported). LSY for H_T indicate that despite these expected changes in ecological function, more genetic diversity is expected to be retained at the total population level (LSY H_T are positive).

Next Decision Analysis estimates the expected LSY assuming that the best choice is made given the expectations under each model. This value equals the expected value of knowing the true dispersal behaviors (i.e., the true model) given the possible choices available:

$$EV[Model|Choice] = \sum_{Model=1}^5 P[Model] * \max(LSY_{Model,Choice})$$

Where, $\max(LSY_{Model,Choice})$ is the largest number of LSY from the six possible choices for each parameterization. If $EV[Model|Choice]$ does not equal $EV[Choice|Model]$ for all parameterizations, then at least one of the five models indicates that a greater conservation benefit can be achieved by making a different choice than suggested when considering all models to be equally likely.

The expected value of learning the true dispersal behaviors can now be estimated as the expected value of perfect information ($EVPI = EV[Model|Choice] - EV[Choice_p|Model]$). If EVPI is positive then reducing uncertainty may lead to a different EP choice that provides greater conservation benefits.

The EVPI is zero for PBG (Table 10). In other words, reducing uncertainty in dispersal would likely not lead to a different preferred choice if one were to only prioritize PBG, given the range of dispersal uncertainty originally evaluated with POM. However, the EVPI is greater than zero for all genetic services. Therefore, the expected conservation value of knowing the true dispersal model is greater than the conservation value of the preferred choice given existing uncertainties. Therefore, despite the application of POM we are still uncertain which EP parcels contribute the most to minimizing habitat fragmentation effects across the Onslow Bight.

Table 10. Results of Decision Analysis for the four ecological services included in LEA (PBG, HS, DST, and HT). Expected Value (EV) is expressed in Landscape Service Years (LSY).

PBG			H _s		
	EV [Choice Models]		EV [Choice Models]		
Bear Garden	4.96		-0.114		
Bear Garden Trans	5.50		-0.0275		
Shaken Creek	2.64		-0.0422		
Shaken Creek Trans	2.65		-0.0455		
Oak Island	2.55		-0.0380		
Oak Island & sGSRA	6.19		-0.0585		
		EV [Model Choices]		EV [Model Choices]	EVPI
		6.19		0.00645	0.0339
D _{ST}			H _T		
Bear Garden	-0.415		0.0262		
Bear Garden Trans	-0.201		0.0321		
Shaken Creek	-0.218		0.0269		
Shaken Creek Trans	-0.225		0.0248		
Oak Island	-0.190		0.0239		
Oak Island & sGSRA	-0.258		0.0262		
		-0.158		0.0341	0.00200

4.2.3.2 Cost-effectiveness

LEA organizes habitat allocation decisions based on the in-kind replacement costs of the ecological services. Hypothetical replacement costs of ecological services were developed in consultation with CL to include costs to preserve land in perpetuity (i.e., fee title or conservation easement), short-term management costs (i.e., restoration during first five years), long-term management costs provided by a non-wasting endowment, and costs to translocate birds. Translocation costs were based on an estimate of \$15,000 per pair and were based on median number of pairs translocated across the five parameterizations (Table 9). For simplicity only total costs are reported here (Table 11).

LEA allows us to incorporate habitat fragmentation effects into cost-effectiveness analysis. The most cost-effective trade is defined as the one providing the greatest conservation benefits at the lowest cost (Wätzold and Schwerdtner 2005). Specifically, the most cost effective trade has the lowest cost per LSY. However, the EP choices available were not expected to replace H_S and D_{ST} services and actually created a net increase in habitat fragmentation. For discussion purposes, cost effectiveness is presented in terms of PBG and H_T only, as these values provided positive estimates for LSY (Table 10).

The most cost-effective choice for increasing PBG is to restore Bear Garden with or without translocation. For Shaken Creek it is more cost-effective not to employ translocation when attempting to increase PBG. Credit values for total genetic diversity (H_T) are much greater than those for PBG, indicating that management decisions that contribute to increased retention of genetic diversity are harder to find. For Shaken Creek, translocation decreases cost effectiveness of LEA credits for H_T considerably.

The EVPI for H_T was greater than zero. Therefore, a cost-effective level of investment in a research study designed to reduce uncertainty in dispersal is estimated as (EVPI * price / credit = $0.002 * \$519,049,644 = \$1,036,679$).

Table 11. Hypothetical costs for EP parcels and results of cost-effectiveness analysis.

	Number of territories	Total Cost	Cost/LSY PBG	Cost/LSY H_T
Bear Garden	45	\$12,257,145	\$2,473,271	\$467,843,390
Bear Garden Trans	45	\$12,963,720	\$2,358,226	\$404,110,396
Shaken Creek	10	\$10,374,000	\$3,930,615	\$386,316,518
Shaken Creek Trans	10	\$10,555,575	\$3,982,091	\$425,083,379
Oak Island	16	\$14,488,000	\$5,684,610	\$607,273,008
Oak Island & sGSRA	38	\$21,550,000	\$3,481,291	\$823,671,169
Average		\$13,698,073	\$3,651,684	\$519,049,644

4.3 Conclusion

The interactions between landscape change and an organism's natural history can generate complex interactions among population processes occurring at different spatial scales. This is particularly problematic when we lack adequate understanding of the population processes affected (e.g., dispersal). We have illustrated how LEA and POM provide a parsimonious approach for evaluating these complex changes occurring at a patch scale (Appendix B) in a manner that reduces the dimensionality into a few credit values, summarizing landscape-scale dynamics, and facilitating decision making.

The range of properties included in this case study varied greatly in habitat area and in connectivity with the existing recovery population. These properties also differed greatly in opportunity costs. Given the possible large dimensionality of this ecological-economic problem the integration of LEA and POM using Decision Analysis may help managers decide to put more negotiating effort into parcels providing strategic connectivity (i.e., Oak Island) or to be large enough to help minimize the influence of genetic drift (i.e., Bear Garden). This may be helpful because natural resource managers have much more experience managing habitat for reproduction than managing the landscape for connectivity, or dispersal. Our approach could even be extended to assign conservation value to forested corridors for dispersal that may never contribute to nesting. These results suggest that the cost of increasing connectivity may be far greater than the cost of providing breeding habitat. Further, our approach highlights that translocation can have negative biological consequences and LEA was able to translate those consequences into the higher credit costs for H_T when translocating birds to Shaken Creek.

This work has illustrated that landscape change may increase erosion of genetic variation within breeding groups. The first step toward estimating the ecological significance of this change, especially given the threshold effects observed with inbreeding depression (Frankham 1995b), would be to collect tissue samples to determine current levels of inbreeding. These genetic data could then also be incorporated with POM to help reduce uncertainty regarding dispersal (Bruggeman et al. in press).

5.0 Application of Pattern Oriented Modeling to Gopher Tortoise

Objective 3 of SERDP RC-1656 was to evaluate the transferability of the LEA/POM technologies by building an IB-SEPM for a species far less studied and having drastically different natural history than the RCW. IB-SEPMs are perhaps most productively viewed as experimental systems that test hypotheses regarding how population patterns emerge from traits of individuals (Grimm and Railsback 2005). Further, constructing an IB-SEPM to include uncertainty regarding components of GT natural history that likely contribute critically to population persistence permits an Adaptive Management approach for conservation. POM provides a mechanism for comparing simulation results with observed data to assess model fit and to test hypotheses regarding how key behavioral and demographic mechanisms are affected by environmental heterogeneity and management decisions. Therefore, IB-SEPMs can contribute critically to the drafting of recovery plans, as has been accomplished for RCWs (USFWS 2003).

We proposed to apply POM through the development of a new technique in landscape genetics, which was beta tested with RCWs (Bruggeman et al. 2010). This technique relates the spatial autocorrelation of land use types, estimated using point pattern statistics, to measures of genetic diversity to infer dispersal parameters. As described below, the technique has been successfully extended to GTs for both empirical and simulated data. The technique has also been developed to estimate model fit to describe the ability of alternative model parameterizations to approximate the relationship between the spatial autocorrelation of habitat and genetic diversity. Further, thanks to collaboration with FB and Auburn University, we have collected more empirical data than we originally thought possible and developed other estimates of model fit. Thus, we have been able to develop a far more detailed IB-SEPM than originally proposed.

5.1 Methods

5.1.1 Model Description

A detailed model description following the ODD method (Grimm et al. 2010) is provided in Appendix C, which includes all model parameters and literature used to assemble model assumptions. Briefly, the simulation represents the locations of adult GT in terms of their home range, or the burrows that they occupy in a year. A yearly time step is applied to the model. Immature tortoises are not known to participate in social interactions, so their location is modeled only as a point on the landscape until they become adults. The home range is a fundamental concept that integrates the location and intra-annual movement of individuals, and social interactions including mating. GT spend up to 90% of their time in underground burrows (Eubanks et al. 2003) and mating encounters typically take place on the burrow apron (Boglioli et al. 2003). Male and female tortoises in the simulation only mate if their home ranges overlap. Overlap occurs when a burrow is included in the both the male and female's home range. Males that overlap with a female's home range contribute to that female's sperm

storage in proportion to the number of burrows that they have in common. Although it is not known precisely how long stored sperm remains viable (Palmer and Guillette 1988, Pearse and Avise 2001), in the simulation it is assumed females store the sperm of males that they overlap with for three years. When a female lays a clutch of eggs, the father of each egg is drawn randomly from the female's sperm storage such that males having greater overlap with a female have a greater likelihood of siring her offspring (Appendix C, Section 7, Assign home range and Reproduction submodels).

Because home range size varies with the density of tortoises, which is proportional to the density of burrows (Guyer et al. 2012), home ranges are constrained in the simulation by limiting the total pairwise distance between burrows in the home range (Appendix C, Section 7, Assign home range submodel). Females do not seek out mating opportunities with males and are not motivated to aggregate together, reflecting our understanding of the GT mating system as scramble competition polygyny (Johnson et al. 2009). Instead, adult males seek to overlap with as many females as possible (thereby maximizing their potential mates). Adults of both sexes also avoid overlapping with members of their own sex.

The simulation is initialized with active and inactive burrows from a burrow survey, and the initial population size is estimated with a conversion factor recently estimated on FB (Appendix C, Section 5, Initialization). This conversion factor is also known as the burrow occupancy rate and is equal to the estimated ratio of tortoises to burrows (Nomani et al. 2008). Throughout the simulation experiment this ratio is maintained by removing burrows from the landscape that are not occupied by tortoises (i.e., that are abandoned) for five years in a row, and by allowing tortoises to add burrows to the landscape when the ratio of tortoises to burrows has risen too high above the conversion factor (see Appendix C, Section 7, Update burrows submodel, for details).

We developed habitat suitability models to describe GT habitat quality in terms of soils, vegetation, distance to roads and waterbodies, and topography within 30 m grid cells across the simulation landscape (Kowal et al. In press; Appendix C, Section 2, Landscape). When tortoises add new burrows in the simulation, they must be added in areas of sufficient habitat quality and within a range of distances of existing burrows (Appendix C, Section 7, Dig burrows submodel). Tortoises also respond to habitat suitability when they undertake long-distance movement from their natal area (emigration) (Appendix C, Section 7, Emigration submodel).

Each year, tortoises experience a fixed probability of emigration that is specific to their sex and lifestage (Appendix C, Section 7, Emigration submodel). Each tortoise is assigned a number of steps that is selected from a sex- and lifestage-specific uniform distribution. The model assumes immature tortoises and adult females are sensitive to habitat quality when ending their emigration path: they may choose to end their path before reaching the end of their allotted steps if they enter an area of high quality habitat. In contrast, the model assumes adult males are sensitive to the proximity of adult females and may end their emigration path early when burrows occupied by adult females are nearby (Appendix C, Section 7, Emigration submodel).

5.1.2 Simulation Experiment

Despite our literature review and data mining from Auburn University's radio telemetry database, there are many aspects of GT natural history that remain poorly understood. To illustrate how POM can be applied to uncertain components of GT natural history, the analysis focuses on two areas of uncertainty here: the mating system and emigration. This section begins by addressing how uncertainty is included in the simulation, and then simulation conditions applied to run POM experiments are described.

5.1.2.1 Mating System Uncertainty

We included alternative submodels to evaluate the ability of different home range assignment rules to approximate summary statistics observed in the field. Both are binary parameters that control structural features of the home range assignment process. Using binary parameters to turn on or off different home range assign processes rules allows us to treat structural uncertainty as parameter uncertainty using POM. The first of these, female site philopatry, simulates extreme site fidelity by adult females. When female site philopatry is enforced, females receive one home range upon maturation to adulthood and continue to occupy the same burrows for the rest of their lives; otherwise (and this is the case for males) home ranges are re-assigned every year, keeping at least one burrow in common with the home range of the previous year (Appendix C, Section 7, Assign home range submodel). Mark-recapture studies of GT populations have demonstrated that some tortoises do exhibit extraordinary site fidelity; some tortoises have been recaptured in the same area where they were first marked up to nearly three decades later (Berish et al. 2012). Recapture rates are also generally higher for females than for males (Diemer and Moore 1993, Berish et al. 2012), suggesting that females may be more likely to display such site fidelity. Importantly, the site philopatry parameter does not influence the probability of emigration by females.

The second alternative home range assignment rule is a parameter simulating mate fidelity by males. Recent analysis by Guyer et al. (unpublished) suggests that the social structure of tortoise colonies may be more complex than previously imagined. The term "clique" has been proposed to describe small social substructures within a tortoise colony, where individuals maintain social connections without regard to spatial proximity (i.e., individuals within small subgroups strive to interact with each other though they may not be neighbors). The male mate fidelity parameter simulates the formation of cliques by motivating males to overlap with females that they overlapped with in the previous year.

5.1.2.2 Emigration Uncertainty

Emigration in the GT, defined here as movement among breeding colonies or to unoccupied habitat, is still very poorly understood. Many practitioners believe that rivers, streams, and heavily traveled roads impede movement. However, a recent range-wide population genetic study suggested that only major rivers (i.e., Mobile R. and Apalachicola R.) were sufficient to impede movement (Clostio et al. 2012).

In order to learn about dispersal, a landscape genetic study was conducted at FB, randomly sampling 100 individuals across a 1 km grid and assaying blood for 32 microsatellite loci (Kreiser et al. 2013). A new technique that relates genetic variation to estimates of habitat density at different lag distances was applied to detect spatial thresholds indicative of underlying population processes (Bruggeman et al. 2010). O-ring indices estimate the density of habitat present within a ring (here 120 m wide) at different lag distances (Appendix C, Section 6A). By correlating O-ring indices with total number of alleles (i.e., TNA~O-ring correlation) observed at each of the sample locations, evidence for female site philopatry and male biased dispersal (Fig. 4) was found, as has recently been suggested for other tortoises (Paquette et al. 2010). These results indicate that the density of habitat at the shortest spatial scale and at intermediate spatial scales is positively associated with greater allelic richness for females. But for males, only correlations at a few intermediate distances were observed. We hypothesize that if females tend to stay close to their natal areas and successfully recruit into adulthood (minimizing drift), this would lead to significant correlations at short lag distances (240 m). And if females tend to disperse short distances and move preferentially within good habitat to move among breeding colonies, this would lead to significant correlations at intermediate lag distances (1.4-3.6 km). Further, if males tend to emigrate at a higher frequency and ignore habitat quality during long distance movement (i.e., male biased dispersal), this would lead to the absence of correlations at longer lag distances.

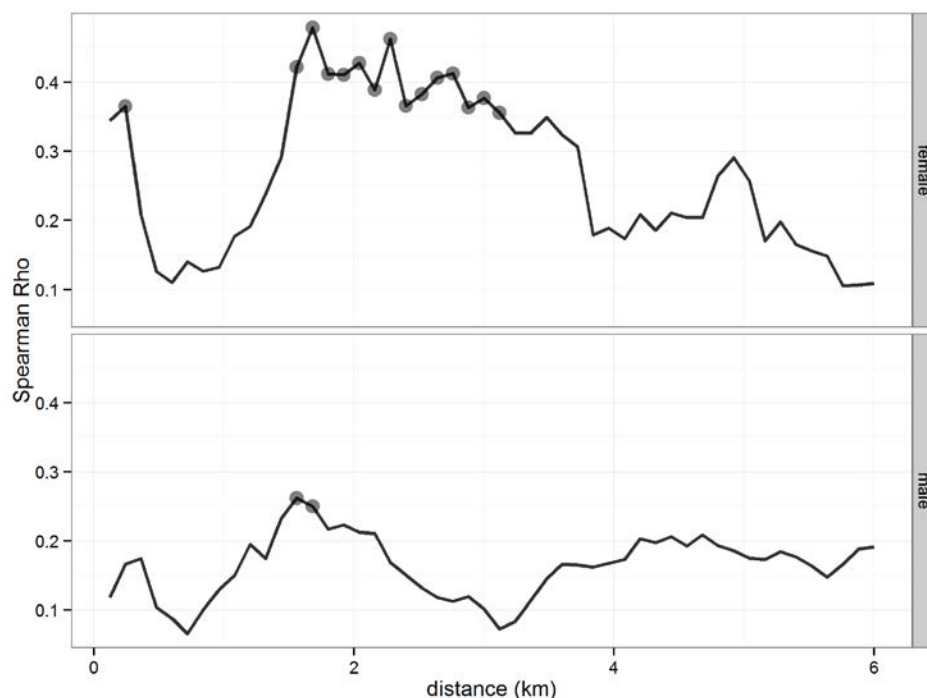


Figure 4. Spearman's Rho rank correlation between total number of alleles for the genetic field samples and O(r,p) for values of r between 120-6000 m. Distance classes with significant correlations have larger points. Significant correlations were identified for females at 240 m and 1560-3120 m, and for males between 1560-1680 m.

POM was used to evaluate these movement hypotheses. Within the IB-SEPM a correlated random walk movement model (Zollner and Lima 1999, Bruggeman and Jones 2008) was applied. The correlated random walk model can be used to weight the importance of straight dispersal, which allows animals to sample more space per unit effort, or friction based dispersal, in which organism tend to move through areas with some preferred characteristic. The model currently assumes that friction is inversely related to habitat quality.

Given the landscape genetic results, we decided to set female dispersal parameter values as constant, based on the literature, and to reflect more limited movement. Direct estimates for probability of emigration and range of movement distances were available for adults of both sexes thanks to past radio telemetry studies (Appendix C, Table C6). However, little is known about movement of juvenile and subadult males. Therefore, the probability of emigrating, dispersal steps, and strength of habitat-based versus directional dispersal was varied for juvenile and subadult males (Table 12). We also allowed strength of habitat-based versus directional dispersal to vary for adult males.

Table 12. Mating system and emigration parameters treated as uncertain in POM simulation experiment.

Parameter	Abbreviation	Range evaluated
Probability of subadult male emigration	Sub. M emigration	0 – 1
Probability of juvenile emigration	Juv. emigration	0 – 1
Subadult male minimum steps	Sub. M min steps	1 – 100 cells
Subadult male maximum steps	Sub. M max steps	101 – 200 cells
Juvenile minimum steps	Juv. min steps	1 – 100 cells
Juvenile maximum steps	Juv. max steps	101 – 200 cells
Adult and subadult male habitat-based movement (β)	M β	0 – 1
Juvenile habitat-based movement (β)	Juv. β	0 – 1
Female site philopatry	F site philopatry	0 [off] – 1 [on]
Male mate fidelity	M mate fidelity	0 [off] – 1 [on]

Each cell = 30 m

5.1.2.3 Simulation Conditions

An important first step of POM is to constrain the model with as much field data describing the starting state of the system as possible (Wiegand et al. 2004). The objective of the POM experiment is to estimate errors in model fit associated with both genetic and demographic data observed on FB from the 2008-2010 time frame (i.e., the time at which observed data describing burrow patterns and population genetics were available). Because empirical demographic data were available to initialize the model in 1999 (i.e., USFWS burrow survey), we ran one experiment from 1999 to 2009 and estimated model errors for demographic patterns only. This will be referred to as the **shortPOM** simulation experiment.

A second POM experiment was run to estimate errors associated with genetic patterns. The genetic structure of the extant population within the boundaries of FB was likely affected by land use change occurring within current boundaries of FB and the area to the northeast along the Chattahoochee Fall Line. Further, the simulation needed to be run for sufficient time to create the possibility for genetic differences to occur across the 31 microsatellite loci included in the TNA~O-ring analysis applied to field data. Others have found significant correlations can result due to barrier effects in simulated microsatellite loci in as few as 10 generations with 30 loci (Landguth et al. 2010). Therefore, we began this experiment by first simulating a population estimated at a pre-European settlement condition (i.e., Pre-settlement, including tortoises outside FB current boundaries) for 500 years, or 14 generations, and then altered demographic parameters at three subsequent times to simulate the impacts of European settlement and subsequent re-establishment of the population on FB (Appendix C, Table C3). This experiment will be referred to as the **longPOM** experiment, as 683 years are simulated (1326-2009).

Due to the drastically different simulation conditions applied between the shortPOM and longPOM experiments, far more parameterizations can be evaluated under shortPOM than longPOM. Therefore, first a shortPOM experiment was run testing the ability of 20,022 parameterizations, iterated 100 times using Monte Carlo methods. Parameterizations were assembled through random stratified sampling with replacement (i.e., Latin hypercube) from the range of values in Table 12. Because longPOM simulates GTs over 683 years and starts with a far greater number of initial burrows (Appendix C, Fig. C3), we can only run three parameterizations in five days. Therefore, we only simulated the three best parameterizations using the longPOM conditions to determine how well they can replicate the relationship between genetic diversity and habitat quality.

5.1.3 Summary Statistics

Summary statistics are observable components of population structure affected by life history traits thought to underlie population persistence (Wood 2010, Martinez et al. 2011). At this stage in GT research we collected as many summary statistics as were available. Summary statistics were derived from data collected at FB when possible and from outside datasets when necessary (Table 13). We quantify the error between observed and simulated summary statistics using the sum of squares (SSq) to rank the fit of alternative model parameterizations (Beaumont 2010). Details describing how the summary statistics were calculated can be found in Appendix C, Section 6A, and will be briefly presented here.

Because home range characteristics contribute critically to the mating system, and thus population growth and the accrual of inbreeding, two different home range characteristics for each sex were derived: number of burrows in the home range and percent of home range overlap with the opposite sex. Observed patterns describing home range size and home range overlap were drawn from an unpublished multi-year, multi-site radio telemetry database from areas outside of FB as no radio telemetry data were available from FB. To compare these

observed patterns with tortoise home ranges in the last year of the POM simulation, the two home range metrics for all adults in the simulated population were summarized.

Another summary statistic describes the spatial autocorrelation, or spatial dependency, of active and inactive adult burrows across the landscape. This is an important summary statistic as it is based on the most common data source for GT (i.e., burrow surveys), and high burrow density is important for the maintenance of GT social interactions (Guyer et al. 2012). Spatial autocorrelation of adult burrows was characterized using O-ring indices (Wiegand and Moloney 2004). Using the 2008-2010 J Carter Burrow survey, O-ring indices were used to measure the average density of points in a point pattern (e. g., a GT burrow survey) contained in ring-shaped regions over a variety of spatial scales. Results indicated that the spatial distribution of adult burrows from the J Carter burrow survey display patterns of spatial autocorrelation at small spatial scales, in which there is a higher probability of finding burrows at short lag distances from other burrows than at long lag distances (Appendix C, Fig. C10). While the mechanisms behind the spatial autocorrelation remain vague, likely due to behavioral interactions and resource partitioning, POM provides a valuable tool for testing mechanisms. The same summary statistic was calculated within POM simulations in 2009 using the burrow pattern generated by each parameterization. Our ability to approximate this summary statistic is indicative of not only our home range assignment rules but also our dispersal assumptions.

The last summary statistic is the Spearman rank correlation between GT genetic diversity and spatial autocorrelation of habitat, which represents an extension of an approach developed for RCWs (Bruggeman et al. 2010). For this method began by calculating TNA from samples collected from 100 individuals across a 1 km grid on FB in 2009 by the University of Southern Mississippi (Appendix C, Section 6A). Then the O-ring statistic was calculated to characterize the spatial autocorrelation of habitat at different lag distances from each of the field sample locations. To determine if male and female genetic diversity had a different relationship with habitat density, correlation between TNA and the O-ring values for habitat on each sex separately was estimated. Within the longPOM simulation, for each Monte Carlo iteration the genetic sampling scheme conducted in 2009 on FB was replicated, but we did not force sampling of the exact location, because after 683 years of simulation the spatial locations of burrows varied such that there were often no tortoises present at the exact field sampling location. After 100 locations were sampled for adults in the simulation the Spearman rank correlation analysis between TNA and O-ring index for habitat was estimated.

Table 13. Sources for observed summary statistics used during the POM simulation experiment.

Abbreviation	Observed Summary statistic	Source
M # bur	Number of burrows in male home range	Guyer telemetry dataset ¹
F # bur	Number of burrows in female home range	
M % overlap	Percent of male home range overlapped by female home ranges	
F % overlap	Percent of female home range overlapped by male home ranges	
Bur O-ring	Univariate O-ring index for adult burrows	JCA burrow survey
TNA~O-ring	Spearman rank correlation between genetic diversity (as Total Number of Alleles) ~ O-ring for habitat	2009 Ft. Benning Genetic Sample & Pre-settlement habitat model

¹C. Guyer unpublished data from Mobile Co. AL, Camp Shelby, and Conecuh National Forest site #4. n=32 male, 30 females. Detailed site descriptions can be found in Guyer et al. (2012).

5.1.4 Data Analysis

In order to evaluate model performance and behavior, Spearman rank correlations were estimated for results from shortPOM. First, to evaluate model performance, correlations between uncertain parameters and primary model predictions (Table 14) were performed. Such an analysis helps to identify which monitoring data are more strongly associated with different processes included in the model, as represented by the uncertain parameter values. Second, to evaluate redundancy and complementarity among different types of summary statistics, correlations among estimates of model fit for different demographic summary statistics included in shortPOM were estimated. The third set of correlations evaluated the contribution of each uncertain parameter to model fit, or the ability of uncertain parameters to reduce errors between observed and simulated summary statistics.

Table 14. Definition of primary model predictions. All values were averaged across 100 Monte Carlo iterations.

Primary model prediction	Definition
# adults	Number of adults in 2009
# subadults	Number of subadults in 2009
# juveniles	Number of juveniles in 2009
# hatchlings	Number of hatchlings in 2009
♂ emigration dist	Average straight-line displacement accomplished by adult male emigrants
♀ emigration dist.	Average straight-line displacement accomplished by adult female emigrants
♂ overlap with ♀	Average percent of male home ranges overlapping females in 2009
♀ overlap with ♂	Average percent of female home ranges overlapping males in 2009
frequency multiple paternity	Average frequency of clutches with multiple paternity in 2009
# sires per clutch	Average number of sires per clutch in 2009
♂ # burrow in home range	Average number of burrows in male home range in 2009
♀ # burrow in home range	Average number of burrows in female home range in 2009

The thesis of POM is that parameters able to simultaneously replicate multiple types of observed data more likely reflect the actual natural history traits (Wiegand et al. 2004, Grimm et al. 2005). Therefore, we evaluated the range of parameter values that results when we demand decreasing errors in SSq for all summary statistics. Recall that due to simulation dimensionality, only three parameterizations can be evaluated in a longPOM experiment. Therefore, to define the three best parameterizations, a restriction filter, or cut-off value, was applied to the distributions of SSq-values for all summary statistics. Requiring that parameterizations be in the upper 0.45 percentile for the distribution of all summary statistics led to three parameterizations. Then restriction filters were applied at the 0.46-0.48 percentiles, as well, to determine how parameter uncertainty might change with increasing amounts of model error.

5.2 Results & Discussion

5.2.1 Influence of uncertain parameters on primary model predictions.

The strength of the relationship between uncertain parameters and primary model predictions varied greatly, but most often the uncertain parameters did not have an overwhelming influence on model performance (Table 15). The biggest exception was observed for the relationship between adult and subadult male habitat-based movement ($M\beta$) and average straight-line displacement accomplished by adult male emigrants (♂ emigration dist), in which a strong negative relationship was observed. Therefore, the more strongly movement rules force males to stay in high quality habitat, the shorter Euclidean distance they cover. This result

indicates that radio telemetry data would be very useful for reducing uncertainty regarding preferences for habitat during movement. $M\beta$ was also positively related to number of sires per clutch and number of burrows in male home range, indicating a biological benefit for habitat-based movement. Strong correlations were also observed between female site philopatry and number of burrows in female home range, frequency of multiple paternity, number of sires per clutch, abundance of hatchlings, juveniles, and subadults. These relationships were all negative indicating that female site philopatry is expected to have negative consequences for reproductive success. Male mate fidelity was strongly, positively associated with number of burrows in male home range and male overlap with females, but was negatively associated with female overlap with males. Therefore, while a greater percentage of male home ranges overlap with females, there are still a larger number of females not overlapping with males, and this leads to negative relationships between male mate fidelity and abundance of hatchlings, juveniles, and subadults.

Many significant ($p < 0.05$) but weaker relationships were observed for probability of subadult male emigration and subadult male maximum steps. Results suggest a weaker influence of juvenile dispersal parameters, but recall the simulation is only running for 11 years, so juveniles are not given much opportunity to contribute to population dynamics.

Table 15. Spearman correlations between uncertain parameters and primary model predictions (n=20,022). For primary model prediction definitions, see Table 14. Significant (p<0.05) correlations are shown in **bold**. All values were averaged across Monte Carlo iterations (n=100).

	# adults	# sub-adults	# juveniles	# hatchlings	♂ emigration dist	♀ emigration dist.	♂ overlap with ♀	♀ overlap with ♂	frequency multiple paternity	# sires per clutch	♂ # burrow in home range	♀ # burrow in home range
Sub. M emigration	-0.32	-0.359	-0.03	-0.054	0.029	0.003	-0.196	-0.182	-0.213	-0.312	-0.248	-0.022
Juv. Emigration	-0.008	-0.187	-0.079	-0.006	0	0.006	0.003	-0.003	-0.008	-0.008	-0.001	-0.005
Sub. M min steps	-0.071	-0.086	-0.002	-0.004	0.016	-0.002	-0.048	-0.039	-0.042	-0.064	-0.054	-0.001
Sub. M max steps	-0.076	-0.09	-0.015	-0.02	0.005	-0.008	-0.024	-0.043	-0.051	-0.063	-0.038	-0.012
Juv. min steps	-0.005	-0.06	-0.03	-0.013	-0.003	-0.007	0.005	0.003	-0.015	-0.014	-0.011	-0.014
Juv. max steps	0.001	-0.035	-0.021	-0.001	-0.007	0.003	0.001	0.002	0.009	0.011	0.007	0.005
M β	0.185	0.061	-0.06	-0.032	-0.986	0.018	0.336	0.284	0.188	0.431	0.488	0.049
Juv β	-0.001	0.068	0.027	-0.013	0	-0.007	0.011	-0.005	-0.011	-0.008	0.008	-0.008
F site philopatry	-0.016	-0.52	-0.574	-0.565	-0.022	0.119	0.435	0.036	-0.823	-0.715	-0.335	-0.866
M mate fidelity	0.007	-0.477	-0.654	-0.668	-0.009	0.006	0.777	-0.866	-0.419	-0.297	0.705	-0.326

5.2.2 Relationship among estimates of model fit.

We found the strongest relationship between estimates of model fit between number of burrows in female home range and the O-ring index for adult burrows (Table 16). Therefore, these summary statistics provide some redundant information as parameterizations able to closely approximate one summary statistic will likely closely approximate the other. This is perhaps not surprising as the model assumes female home range patterns drive male home range patterns and the spatial autocorrelation of adult burrows is an emergent property of both male and female home range properties. In contrast, the negative relationship observed between number of burrows in a home range and percent of overlap for both sexes provides evidence for pattern complementarity. Therefore, parameterizations able to closely approximate one home range characteristic do a poor job of replicating the other home range characteristic. Thus, multiple summary statistics are needed to characterize home ranges.

Table 16. Spearman correlations among SSq estimates from shortPOM (n=20,022).

	SSq error, F # burrows	SSq error, M % overlap	SSq error, F % overlap	SSq error, Bur O-ring
SSq error, M # burrows	0.185*	-0.603*	0.120*	0.242*
SSq error, F # burrows		0.540*	-0.222*	0.851*
SSq error, M % overlap			-0.494*	0.592*
SSq error, F % overlap				-0.475*

* p < 0.05

5.2.3 Contribution of uncertain parameters to model fit.

Correlations with our two binary variables (i.e., female philopatry and male fidelity) were the strongest (Table 17), suggesting that choice of submodels has a strong impact on the ability of the model to approximate observed summary statistics. Results indicate that male mate fidelity was strongly, positively correlated with percent of female overlap. Therefore, when the male mate fidelity submodel was turned on, the IB-SEPM did a poor job of approximating female overlap with males. In contrast, turning male mate fidelity on allowed the IB-SEPM to do a better job of approximating percent of male burrow overlap with females (i.e., a negative relationship was observed). When female site philopatry was turned on, the IB-SEPM did a better job of approximating number of burrows in female home range and spatial autocorrelation of adult burrows (i.e., negative relationship).

We also found a strong positive relationship between tendency of subadult and adult males to follow habitat-based dispersal rules and the error associated with the number of burrows in a male's home range, indicating that habitat-based dispersal rules increase the errors for these patterns. However, male habitat-biased dispersal rules decrease the errors for predicting percent overlap for both sexes. Higher probability for subadult male emigration decreases

errors associated with number of burrows in male's home range, but increases errors for percent overlap for both sexes.

Table 17. Spearman correlations between uncertain parameters and SSq estimates from shortPOM (n=20,022).

	SSq error, M # bur	SSq error, F # bur	SSq error, M % overlap	SSq error, F % overlap	SSq error, Bur O-ring
Sub. M emigration	-0.330*	-0.017*	0.194*	0.193*	-0.103*
Juv. emigration	0.000	-0.005	-0.003	0.003	-0.006
Sub. M min steps	-0.068*	-0.003	0.048*	0.041*	-0.017*
Sub. M max steps	-0.052*	-0.012	0.024*	0.044*	-0.027*
Juv. min steps	-0.010	-0.013	-0.005	-0.003	-0.017*
Juv. max steps	0.008	0.004	-0.002	-0.002	0.007
M β	0.639*	0.030*	-0.340*	-0.300*	0.248*
Juv. β	0.007	-0.006	-0.011	0.005	-0.011
F site philopatry	-0.317*	-0.866*	-0.408*	-0.041*	-0.832*
M mate fidelity	0.504*	-0.249*	-0.789*	0.866*	-0.461*

* $p < 0.05$

The observation that some parameter values are positively associated with errors in model fit and others are negatively associated is not surprising. IB-SEPMs are complex, simulating the interaction among multiple biological processes.

By demanding increasing agreement between observed and simulated data for all summary statistics (Fig. 5), uncertainty in all parameters related to the mating system and male subadult and adult dispersal decreased. As we demand better fitting parameters, the probability of subadult male dispersal goes to zero in two out of three parameters. Therefore, estimates of minimum and maximum steps do not contribute to model fit for these parameters, as subadult males are not moving. Strength of habitat-based movement rules for subadult and adult males

decreases as better fitting models are required by the filters, which tends to agree with genetic analysis indicating female philopatry and male biased dispersal (Fig. 4). Similarly, results indicate that female site philopatry was selected but male mate fidelity was turned off across all rejection filters.

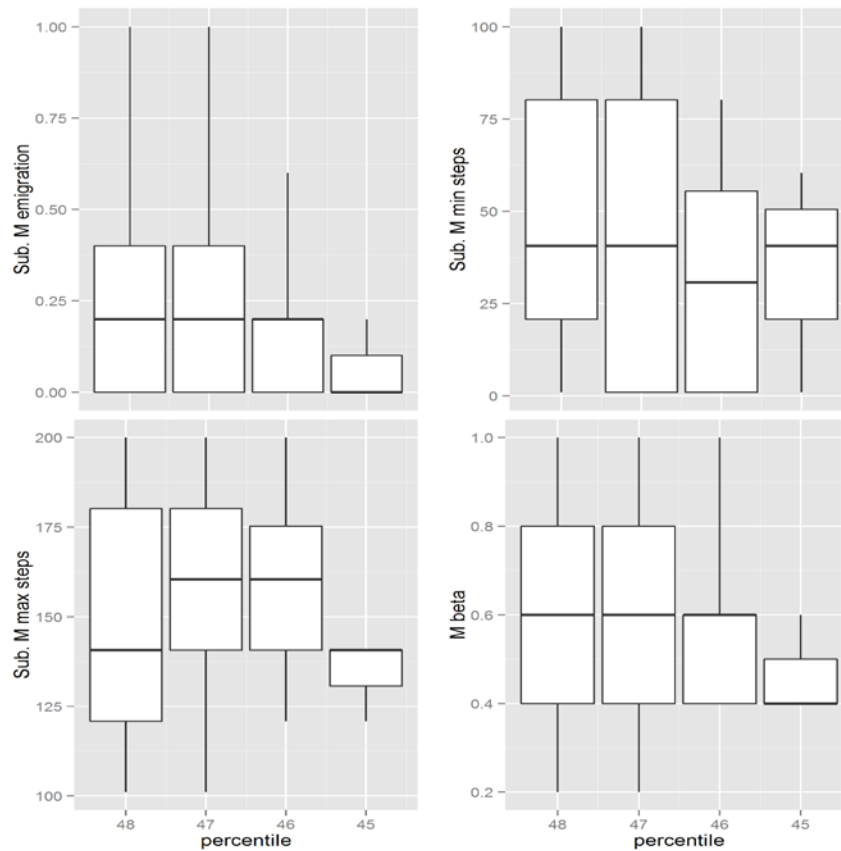


Figure 5. Change in parameter values that result as we demand greater agreement between observed and simulated summary statistics. The number of parameters within the 0.48 percentile = 77; within 0.47 percentile = 35; within 0.46 percentile = 10; within 0.45 percentile = 3. Only uncertain parameters for subadult and adult dispersal are presented because male juvenile tortoises were not given sufficient time to affect estimates of model fit over 11 years. Across all percentiles, parameters that minimize SSqs turned female philopatry on and male mate fidelity off.

5.2.4 Ability of best parameterizations from shortPOM to replicate genetics patterns using longPOM

For the three-best parameterizations remaining after shortPOM (i.e., parameters able to satisfy the 0.45 percentile restriction filter), we found that none were able to replicate the peaks in correlations at specific lag distances observed for the empirical sample (Figs. 4, 6, 7). This is perhaps not surprising as we were unable to replicate the exact sample locations used in the field (Appendix C, Section 6A). Even when sample size was increased in the simulation up to 400 (i.e., four times the number of tortoises collected in the field) specific peaks were not observed. However, increasing sample size decreased the variation around the mean

Spearman rho, as one would expect, and the mean was very close to that observed with 100 samples (Fig. 6, Fig. 7). The observation of peaks in our empirical samples likely represents phenomena specific to the sample locations, specific time-series of events, a set of life history traits not included in the simulation, or a combination of these factors. However, we argue that contrasting the empirical TNA~O-ring correlation with the average TNA~O-ring correlation generated across Monte Carlos by each parameterization, using the SSq calculation, is still indicative of the model's ability to replicate realistic natural history traits.

POM1 did the best job of approximating the empirical relationship between TNA~O-ring index for habitat for males, but the best fit for females was POM2 (Table 18). The change in errors for demographic summary statistics between longPOM and shortPOM were also contrasted (Table 18). The demographic errors most often increased in longPOM compared to shortPOM, which is not surprising given the much longer time frame simulated. The exceptions were number of burrows in a male's and female's home range, especially for POM1 and POM2. This may reflect that our home range initialization process is better suited to initializing home range under abundant habitat (i.e., pre-settlement map believed to represent 1326) than when habitat is more scarce (i.e., abiotic map believed to represent 1999). However, errors increased the most under longPOM for percent male overlap with females and percent female overlap with males for POM0, which corresponds to the trend in errors for genetic summary statistics for males.

Because so few parameterizations could be simulated with longPOM, it is difficult to know which uncertain parameters affect these results. We suspect that because we found such strong correlations between subadult and adult habitat-based dispersal ($M\beta$) and estimates of model fit (Table 17), and both POM1 and POM2 set juvenile habitat-based dispersal to 0.8, while POM0 set $J\beta$ to 0, that juvenile dispersal may contribute critically to population structure. The greater error observed for the female genetic summary statistic may be due to much greater probability of subadult male migration included in POM1 than POM0 or POM2 (Appendix C, Table C5). Greater emigration by subadult males may increase the loss of genetic diversity in both males and females due to unsuccessful movements of subadult males that prevent them from becoming breeding adults.

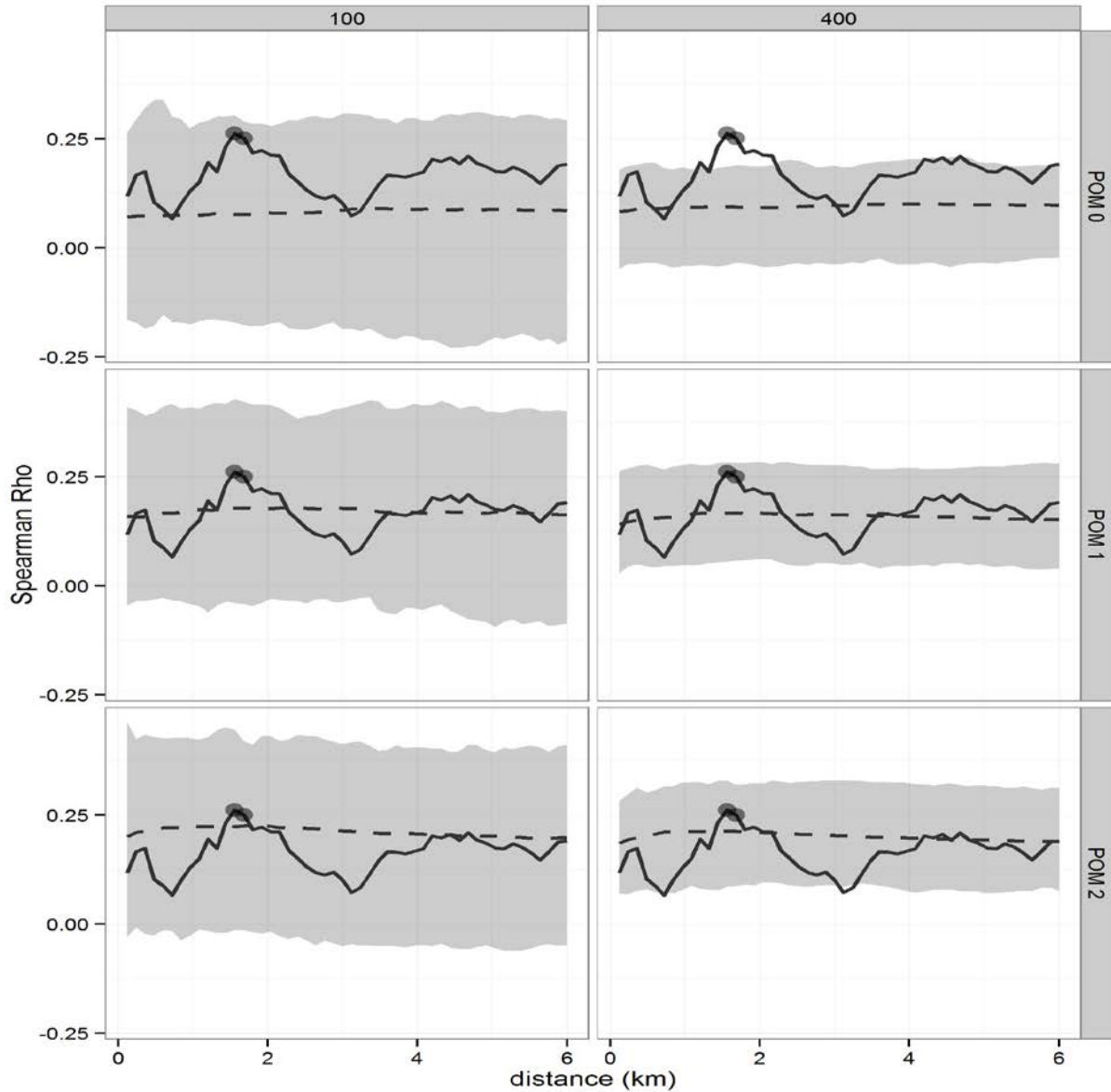


Figure 6. Spearman correlation values for **males** describing the relationship between total number of alleles and O-ring index for habitat. Solid black line represents correlations estimated from empirical genetic samples collected on FB (69 males & 31 females), where the dots on that line represent statistically significant correlations ($p < 0.05$). Black dotted lines represent mean correlation values estimated from the simulation, and the gray represents 95th percentiles of results. We were unable to sample the exact locations in the simulation as that chosen in the field, so random samples of 100 (69 males & 31 females) and 400 (276 males & 124 females) were selected by applying the same sampling grid as was used in the field.

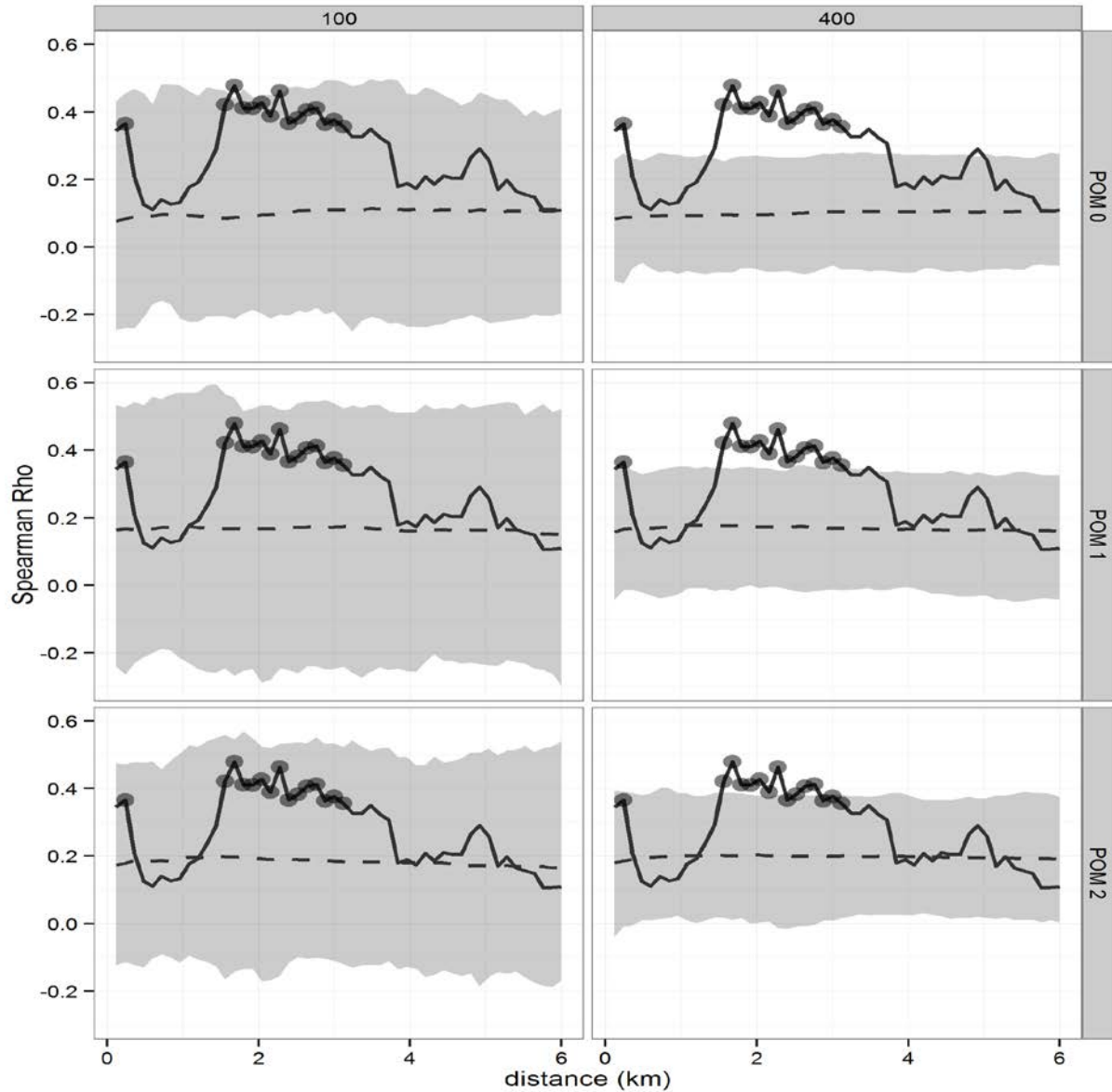


Figure 7. Spearman correlation values for **females** describing the relationship between total number of alleles and O-ring index for habitat. Solid black line represents correlations estimated from empirical genetic samples collected on FB (69 males & 31 females), where the dots on that line represent statistically significant correlations ($p < 0.05$). Black dotted lines represent mean correlation values estimated from the simulation, and the gray represents 95th percentiles of results.

Table 18. SSq error estimates of model fit for the three best parameterizations selected from shortPOM and applied to longPOM.

	ShortPOM			LongPOM		
	POM0	POM1	POM2	POM0	POM1	POM2
SSq error, M # bur	0.135	0.136	0.136	0.088	0.075	0.090
SSq error, F # bur	0.079	0.079	0.079	0.077	0.039	0.037
SSq error, M % overlap	0.158	0.159	0.159	0.440	0.232	0.154
SSq error, F % overlap	0.155	0.149	0.143	0.381	0.129	0.118
SSq error, Bur O-ring	0.002	0.002	0.002	0.014	0.014	0.014
SSq error, TNA~O-ring (M)	NA	NA	NA	1.207	0.803	0.974
SSq error, TNA~O-ring (F)	NA	NA	NA	1.879	2.099	1.587

5.3 Conclusion

We have constructed an IB-SEPM for the GT that includes details of their natural history, including demographic and movement stochasticity, and illustrated the ability of model predictions to approximate multiple data types commonly collected in the field. While much uncertainty remains regarding how GT natural history traits are affected by habitat quality and environmental stochasticity, we have provided detailed results highlighting how our existing model assumptions relate to model predictions. The model does not appear to suffer from severe structural error.

The relationship between parameter uncertainty and estimates of model fit varied, indicating that different types of monitoring will inform us of different biological processes. The strength of the relationship observed with habitat-based dispersal (β) was interesting and suggests that inverse modeling may be very useful for understanding tortoise movement behavior. However, we did not find strong relationships with emigration distances, which may be due to the long lifetime dispersal distances possible for this species or due to structural uncertainty in our movement model. The mating system parameters had the biggest impact on our ability to approximate monitoring data collected in the field. Errors associated with monitoring data derived from radio telemetry studies (e.g., SSq M # bur) displayed the most consistent correlations with the uncertain dispersal parameters (Table 17). Error associated with burrow survey data (i.e., SSq Bur O-ring) was strongly correlated with a few uncertain parameters (i.e., M β , F site philopatry, and M mate fidelity). Therefore, while burrow surveys will likely be more readily available than radio telemetry studies, these results suggest that burrow surveys alone will not be sufficient to learn about GT natural history. However, much work remains to determine the level of model complexity required to inform management decisions, but we believe that this IB-SEPM and the POM framework will be very useful for learning about GT natural history.

Though we believe the model emulates a mating system of female philopatry and male biased dispersal, we were not able to closely approximate the Spearman rank correlation between

total number of alleles and the spatial autocorrelation of habitat for both sexes. “TNA~O-ring” may be thought of as a high level pattern integrating several biological processes with landscape history. The pattern is consistent with a mating system of female philopatry and male biased dispersal, as has been observed in related taxa (Paquette et al. 2010). However, there are likely interactions between the species’ social system and changes in habitat quality that we are simply unable to include in the model at this time. For example, the probability of dispersal may be driven by interactions between habitat quality and social interactions. For the longPOM experiment the pre-settlement habitat map was used to initialize the simulation and to evaluate genetic summary statistics, as we felt this map would likely be most germane for genetic processes. In longPOM we then imposed landscape change by changing demographic parameters (Appendix C, Table C3) but land use did not change because there is much uncertainty concerning how land cover patterns might have changed over 683 years. Certainly, much more work could be completed here, but we believe we have created a valuable framework with which to test hypotheses regarding GT natural history.

6.0 Application of Landscape Equivalency Analysis to the Gopher Tortoise

As illustrated in the section describing application of Decision Analysis to habitat allocations for RCWs, even if model uncertainty remains, LEA & POM can be integrated to weigh alternative decisions. Such decisions may include forgoing a management action to collect more data so that managers can be more confident that the action will lead to the desired outcome. After our efforts here, it is not surprising that the GT natural history is still more poorly understood than RCWs. However, this section illustrates how the techniques can be used to move the uncertainty forward in decision making to form the basis of a good policy instrument, which requires recognizing the influence of uncertainty on decisions.

Much like RCWs, it is believed GTs evolved to exploit upland areas with well drained soils that occur in large expanses across the Southeast. However, unlike RCWs, their populations are not spatially subdivided due to a mating system, though much remains to be learned about GT mating systems. Further, the mechanisms by which habitat fragmentation, independent of habitat loss, might threaten population viability are not understood for this species. One threat may be inbreeding, which results in the loss of genetic diversity by decreasing the frequency of heterozygous genotypes, and has been correlated with reduced survival and fecundity in naturally outbreeding species (reviewed in Frankham 2005). Low levels of genetic diversity have been found in the western range in areas also experiencing low reproductive success, but the link between molecular estimates of inbreeding and reduction in fitness have not yet been elucidated (Ennen et al. 2010).

It is critical to remember that deterministic threats such as habitat loss and fragmentation can have a large impact on how much genetic diversity is retained within a population (Lande 1998, Manel et al. 2003). Studies of populations in natural, undisturbed landscapes describe how natural history traits respond to landscape structure. These studies indicate that species balance rates of recruitment and migration to prevent local extinction, inbreeding and outbreeding depression, and to maintain genetic variance needed for adaptation through natural selection (Mills and Allendorf 1996, Dobson et al. 1997, Storz 1999, Coltman et al. 2003). We, LEA was devised as a tradable credit system that incorporates a “spatially-explicit” planning objective as the allocation of habitat yielding similar levels of neutral genetic variation observed prior to habitat loss and fragmentation, or a “baseline landscape” (Meffe 1996, Bruggeman et al. 2005, 2009). The genetic variation observed in a baseline, or pre-settlement, landscape, is indicative of rates of recruitment and migration that maintain adaptive genetic variance and prevent inbreeding and outbreeding depression. LEA quantifies changes in fragmentation by comparing the genetic variation before and after the trade to that observed in this baseline condition (Bruggeman et al. 2005, 2009).

LEA was designed to estimate the conservation value of habitat at the local scale based on its contribution to regional population viability. LEA says that a habitat patch restored is equivalent to a patch lost if the alternative landscape structures before and after the trade are equivalent in terms of 1) abundance and 2) genetic variation measured at the regional scale.

Valuing habitat based on marginal changes in abundance and genetic variation estimated at the regional scale provides a generally-applicable, landscape-scale accounting system to capture interactions between local and regional biological processes (e.g., recruitment and migration) when land cover changes over time. LEA is an extension of resource-based compensation (Jones and Pease 1997) applied to a landscape scale. This analysis assumes that the ecological services that provide these benefits are abundance and genetic variation (Loomis and White 1996, Bruggeman et al. 2005). The financial value of tradable credits under LEA equals the in-kind replacement costs of ecological services that are differentially affected by changes in habitat area and connectivity (Bruggeman et al. 2005).

LEA is performed by comparing temporal trajectories of ecological services from alternative landscape treatments. The landscape treatments represent alternative choices that might be made regarding how habitat maybe lost, restored, or otherwise managed. The LEA approach for GTs differs a little from that presented for RCWs; because the species is not listed, no recovery goal has been determined. Therefore, the first landscape treatment is simply a “Status quo” landscape, which assumes no change in habitat for GT. The second landscape treatment is a “removal” landscape that simulates the loss of habitat and removal of all tortoises from the area. The third landscape is a “relocation” landscape that moves all tortoises from removal areas into lands already protected by the Army’s ACUB program. Management guidelines applied to GT relocation vary by state and their contribution to population viability is far less understood than for species like RCWs. However, application of LEA requires codifying guidelines in a simulation before the conservation community has had a chance to reach an agreement about their value. We believe that LEA will help estimate the conservation value of these management guidelines.

6.1 Methods

6.1.1 Model Description

As described in the GT ODD the natural history traits simulated for POM and LEA are the same (Appendix C, Section 3). However, because LEA is a form of projection analysis simulating population dynamics from 2009 to 2108, an increasingly important parameter for LEA is the nest predation rate, which has long been recognized as a management concern for GTs. The nest predation rate was derived by averaging estimates across multiple studies (Appendix C, Table C6). There are also important differences regarding how the simulation is initialized. While the POM simulation is initialized with burrows surveyed on FB in 1999, the LEA simulation experiment is initialized with locations from burrow surveys covering FB and two ACUB properties owned by TNC. The FB survey was conducted in 2008-2010 by John Carter and Associates, and burrows in unsurveyed areas were estimated using a method in point pattern reconstruction called simulated annealing (Appendix C, Section 5B). A burrow survey of the Brown Springs TNC property was conducted in 2010 by FB Conservation Crew Staff, and the Blackjack Crossing TNC property was surveyed in 2010 by staff of the Joseph W. Jones Ecological Research Center.

6.1.2 Landscape Treatments

6.1.2.1 Status Quo

The status quo landscape represents the habitat availability and land use patterns in 2009, and projects demographic and genetic components of the population for 100 years assuming no landscape change. Recent relocations that took place on FB in 2009 and 2010 were included as part of the Status quo landscape. These historical events were recreated from data provided by FB staff depicting the locations of burrows where tortoises were trapped for removal, and areas where tortoises were relocated (Fig. 8). During recent relocations, the model assumed tortoises were not placed in pens but instead were simply released in high quality habitat: further details of the simulated recent relocation process are in Section 5D of Appendix C.

6.1.2.2 Removal

The removal landscape treatment is the same as the status quo except that it simulates the removal of GT habitat, for example due to construction projects. The model simulates the complete destruction of habitat within removal areas by changing habitat suitability values inside the areas to zero and barring tortoises from re-establishing burrows there (Appendix C, Section 5D). When the removal landscape treatment was applied two different habitat removals were contrasted:

The **Single Large Habitat Removal** landscape describes the removal of tortoises from one large (1,719 ha) rectangular area on FB (Fig. 9). The size of the removal area is approximately equal to the size of the combined removal areas utilized in the recent relocations, and therefore is comparable to the size of areas where tortoises were removed from FB in the past. The removal area intersects 497 of the burrows present at the start of the LEA simulation.

The **Multiple Small Habitat Removal** landscape describes the removal of tortoises from eight small rectangular areas which together have a combined area equal to that of the single large habitat removal area (Fig. 9). The eight small removal areas also intersect a total of 497 burrows used to initialize the LEA simulation (equal to the number of burrows contained by the single large habitat removal).

6.1.2.3 Relocation

We used the guidelines of the Florida Fish and Wildlife Conservation Commission to structure the relocation process (Florida Fish and Wildlife Conservation Commission 2008; see Appendix C, Section 5D, for relocation details). Tortoises of all lifestages (including hatchlings) were removed from removal areas, including adults that occupied any burrows inside the removal area, and relocated to temporary acclimation pens inside ACUB sites. This study contrasted the ability of two ACUB properties to receive tortoises and contribute to regional population viability.

The **Blackjack Crossing Relocation** landscape describes the relocation of tortoises from a habitat removal area on FB to an area of high quality habitat on the Blackjack Crossing TNC

property, a large (3,354 ha) property on ACUB that is distant from FB (Fig. 9). The recipient site capacity of Blackjack Crossing was calculated from the distribution of habitat scores inside the property (Appendix C, Section 5D) to be 6,115 subadult and adult tortoises, but the 2010 burrow surveys conducted by Jones Ecological Research Center staff (using the occupancy rate recently estimated on FB, Staff of Fort Benning Conservation Branch 2012) suggest an existing population of 128 adult and subadult tortoises. In the simulation, the number of adult and subadult tortoises currently occupying the Blackjack Crossing property at the time of the relocations was subtracted from the site capacity.

The **Brown Springs Young Rd Relocation** landscape describes the relocation of tortoises from a habitat removal area on FB to an area of high quality habitat on the Brown Springs Young Rd TNC property. This property is small (160 ha) and is adjacent to the eastern border of FB (Fig. 9). The capacity of the Brown Springs Young Rd property was calculated from the distribution of habitat scores (Appendix C, Section 5D) to be 740 subadult and adult tortoises, but the 2010 burrow survey conducted by FB Conservation Crew staff (together with the occupancy estimate on FB in 2012) suggest an existing population of 32 adult and subadult tortoises. Therefore, when relocations to Brown Springs Young Rd property are simulated, the number of adult and subadult tortoises currently occupying the property at the time of the relocations is subtracted from the site capacity.

6.1.2.4 Pre-settlement / Baseline landscape

The **Pre-settlement landscape / Baseline landscape** is used to estimate rates of genetic drift and inbreeding observed prior to habitat loss and fragmentation on FB. Therefore, the same pre-settlement landscape that was developed to initialize the longPOM experiment was used, incorporating estimated ancestral habitat suitability and estimated burrow locations (Appendix C, Section 5B). In contrast to the longPOM experiment, which ran for 683 years, the Baseline landscape was only simulated for 100 years.

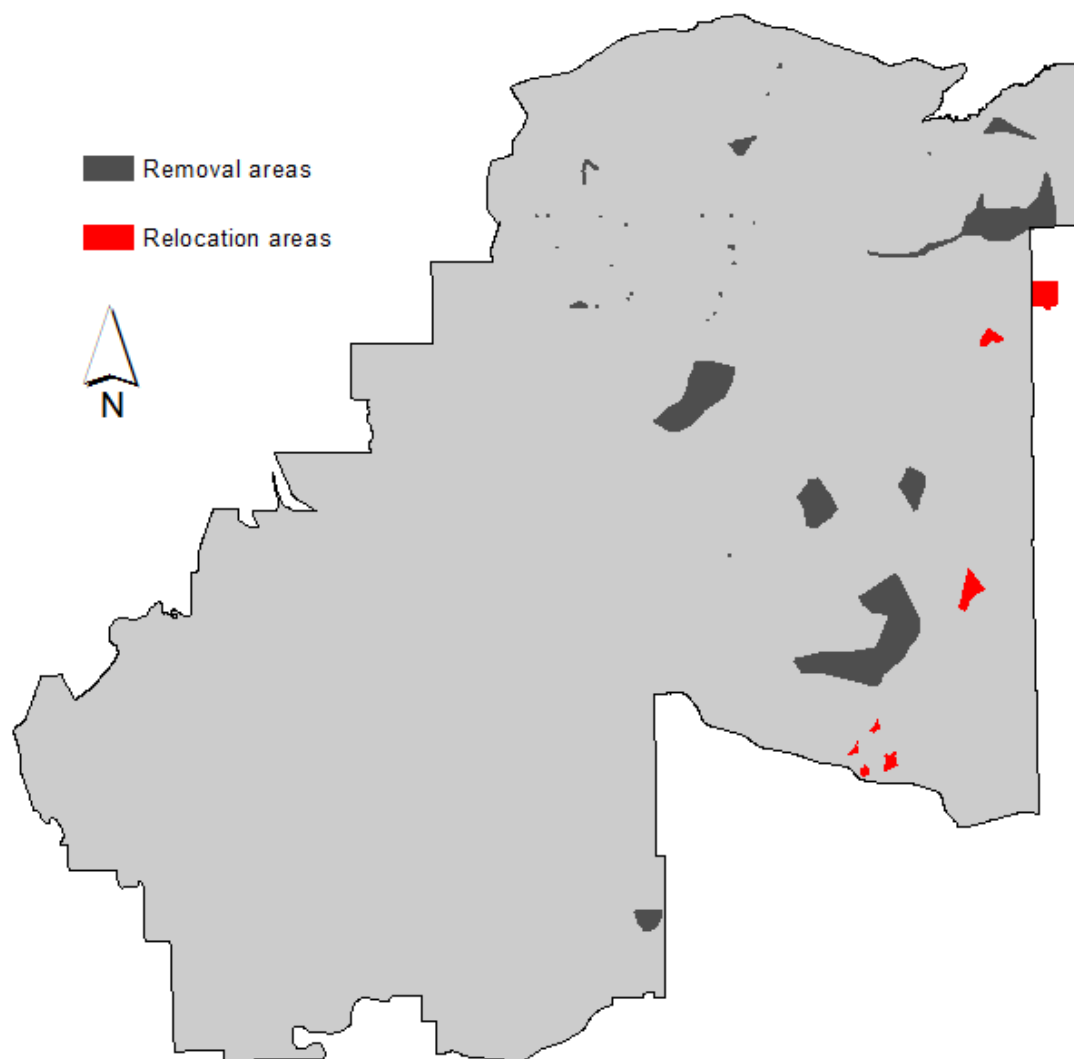


Figure 8. Removal and relocation areas of Ft. Benning comprising simulated recent relocations included in status quo landscape.

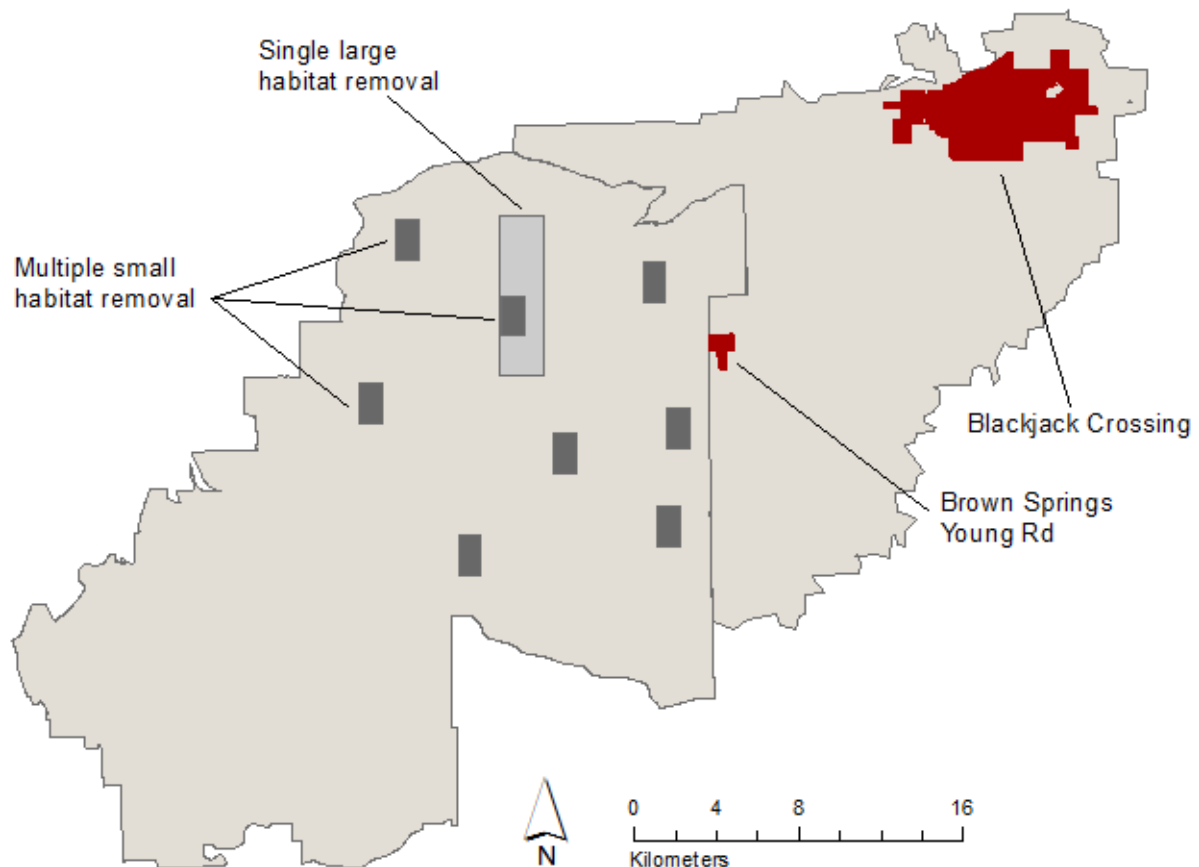


Figure 9. Location of removal and relocation properties used in landscape treatments. Two relocation areas (red) were located on ACUB; removal areas (grey) are shown on FB. The single large habitat removal (light grey) was of equal size, and intersected an equal number of initial burrows, as the combined eight multiple small habitat removal areas (dark grey).

6.1.3 Management Scenarios

LEA estimates debits/credits by comparing ecological service flows from alternative landscape configurations (described above) that are combined into what perhaps can most productively be thought of as management scenarios. The scenarios below represent different options for habitat removal and relocation of tortoises simulated over a 100-year time frame. Each scenario was iterated 100 times in a Monte Carlo simulation using the three best dispersal parameterizations identified in POM.

Single large removal with relocation to Blackjack Crossing (Scenario 1)

Under this scenario, in year 2029 tortoises in the single large habitat removal area are removed from the landscape and relocated to Blackjack Crossing.

Multiple small removals with relocation to Blackjack Crossing (Scenario 2)

This scenario is the same as the single large removal with relocation of tortoises to Blackjack Crossing, except that the removal area consists of eight small areas, which together equal the size of the single large removal, scattered across the installation.

Single large removal with relocation to Brown Springs Young Rd (Scenario 3)

Under this scenario, tortoises are removed from the single large removal area and relocated to the Brown Springs Young Rd TNC property in year 2029.

Multiple small removals with relocation to Brown Springs Young Rd (Scenario 4)

Under this scenario, tortoises are removed from the multiple small removal areas and relocated to the Brown Springs Young Rd property in year 2029.

6.1.4 LEA Calculations

The expected number of abundance credits and debits is estimated as $LSY - \text{Abundance}$ (LSY_c^N ; LSY_d^N):

$$E[LSY_d^N] = \sum_{t=W}^{100} \left(\frac{j_t^N - w_t^N}{r_t^N} \right) \quad E[LSY_c^N] = \sum_{t=W}^{100} \left(\frac{m_t^N - j_t^N}{r_t^N} \right)$$

where W is the time when habitat management is applied (here it is assumed habitat removal and relocation occur at the same time), r_t^N is the expected total abundance expected at **recovery**, j_t^N is the expected total abundance at year t provided by the **status quo** landscape, m_t^N is the expected total abundance at year t provided by **relocating** tortoises, and w_t^N is the expected abundance at year t provided by the landscape including the habitat **removal** landscape. So far, no recovery goal has been determined for GT; nor has the size class used for conservation decision making been determined. This analysis assumes a recovery goal is based on the number of adult tortoises, because they have the highest reproductive value, and this goal at FB is assumed to be 1287 adult tortoises to illustrate the LEA technique. This is the expected number of adults present on FB at the initialization of the LEA simulation (Appendix C, Table C4), so applying this number as a recovery goal implies maintenance of population size over the 100 projected years, which we recognize is debatable.

Calculating credits associated with changes in genetic variance is more complex. The management goal is to approximate population services provided by the distribution of habitat in which the organism evolved, thereby providing an estimate of the extent to which habitat management reduces fragmentation (Bruggeman et al. 2005). As estimates of genetic variance move closer to pre-settlement levels due to restoring habitat area or connectivity, the more credit is accrued in the bank. The credits and debits representing a marginal change in genetic services associated with landscape management can be calculated as $LSY - \text{Genetic Variance}$ (LSY_c^{Ht} ; LSY_d^{Ht}):

$$E[LSY_d^{Ht}] = \sum_{t=W}^{100} \left(\frac{|p_t^{Ht} - w_t^{Ht}|}{p_t^{Ht}} \right) - \sum_{t=W}^{100} \left(\frac{|p_t^{Ht} - j_t^{Ht}|}{p_t^{Ht}} \right)$$

$$E[LSY_C^{Ht}] = \sum_{t=W}^{100} \left(\frac{|p_t^{Ht} - j_t^{Ht}|}{p_t^{Ht}} \right) - \sum_{t=W}^{100} \left(\frac{|p_t^{Ht} - m_t^{Ht}|}{p_t^{Ht}} \right)$$

where H_T is the expected heterozygosity in the total population, p_t^{Ht} is the expected level of genetic variance at year t provided by the **pre-settlement** landscape, j_t^{Ht} is the expected level of genetic variance at year t provided by the **status quo** landscape, m_t^{Ht} is the expected level of genetic variance at year t provided by the **relocation** or mitigation landscape, and w_t^{Ht} is the expected level of genetic variance at year t reflecting anticipated loss of habitat area or connectivity in the habitat **removal** landscape.

LSY_D^{Ht} represents the increase in drift and inbreeding above what is observed in the status quo landscape due to the removal of habitat and tortoises from the population. Therefore, this represents the unmitigated damage to the population if subsequent relocations are not performed. LSY_C^{Ht} represents the extent to which relocation of tortoises onto ACUB lands helps to limit erosion of genetic variation due to drift and inbreeding.

6.1.5 Random Permutation Testing

We use 100 Monte Carlo simulations to estimate distributions describing the expected influence of alternative landscape treatments on ecological structure and function. Therefore, this report focuses on presenting mean expectations generated from the IB-SEPM. Additionally, the null hypothesis that any differences in distributions generated from alternative model landscape treatments result due to chance was tested by employing random permutation testing (Manly 1986). Accepting the null hypothesis means that the two distributions are equally likely despite the removal of habitat, for example. The p-values presented are then inversely related to the strength of evidence against the null hypothesis.

We compared the distribution of adult abundance and H_T observed at year 100 across the 100 Monte Carlo iterations in the three landscape treatments (i.e., status quo, removal, and relocation). To test if the difference in abundance between status quo and removal landscapes, for example, are significant, a distribution of randomly generated median differences was generated by pooling the 100 iterations across landscape treatments and estimating “random” medians by taking two random samples, ignoring treatment labels, of 100 results, 10,000 times. The distribution of random medians was then used to estimate the probability of observing the median difference between landscape treatments if the difference were due to chance.

6.2 Results & Discussion

The probability of total population extinction was zero under all landscape treatments, but a precipitous decline in abundance is expected for the status quo landscape for all parameterizations evaluated here (Fig. 10). Because the status quo landscape anticipates no change in habitat quality, this decline is driven by the expected nest predation rate included in the model (Table C6). Also, only genetic results for locus 1 are presented in this section (Fig. 11; Appendix C, Section 7, Population genetic statistics). Locus one assumes an IAM of genetic

variation such that all founders are unrelated in year 2009; therefore all landscape treatments begin with no initial pattern of genetic diversity to facilitate comparisons of changes in drift and inbreeding across treatments.

6.2.1 Scenario 1: Single large removal with relocation to Blackjack Crossing

Based on random permutation testing of simulation results, the single large removal is expected to decrease the number of adults over time and increase the erosion of total genetic variation leading to LEA debits > 0 (Table 17; Fig. 11). The credit values for scenario 1 reflect the conservation benefit of immediately relocating tortoises following removal, but the expected abundance in status quo and relocation landscapes did not differ significantly based on random permutation testing. Therefore, relocation to Blackjack Crossing may be argued as a sufficient means of mitigating the impacts of a single large removal for abundance. In contrast, the credits were negative and the median expected H_T in status quo and relocation landscapes were statistically different based on random permutation testing for all parameterizations. Therefore, one could argue that despite relocation, the scenario is expected to increase the erosion of genetic variation.

6.2.2 Scenario 2: Multiple small removals with relocation to Blackjack Crossing

In contrast to the single large removal, multiple small removals lead to greater debits for abundance (Table 19). This result suggests that GT may be more sensitive to effects of habitat fragmentation than habitat loss (further evidence contradicting Fahrig 2003, see also Bruggeman et al. 2010), as both scenarios remove the same amount of habitat (i.e., effects of fragmentation were independent of habitat loss). In contrast to Scenario 1, abundance credits for Scenario 2 suggest that relocation to Blackjack Crossing may not be sufficient to offset multiple small removals for POM0 and POM2 (Fig. 10). The credits for H_T were all negative, indicating that relocation is expected to increase the erosion of genetic variation for all parameterizations.

6.2.3 Scenario 3: Single large removal with relocation to Brown Springs Young Rd

Contrasting scenario 1 and scenario 3 suggests that Brown Springs Young Rd provides a similar conservation benefit compared to Blackjack Crossing, as no significant difference in abundance between the status quo and relocation landscape were observed in either scenario (Table 19). However credits for H_T suggest stronger erosion of genetic variation would result if tortoises were relocated to Brown Springs Young Rd compared to Blackjack Crossing (Table 19; Fig. 11).

6.2.4 Scenario 4: Multiple small removals with relocation to Brown Springs Young Rd

Contrasting scenario 2 and scenario 4 suggests that Brown Springs Young Rd may have a higher conservation value than Blackjack Crossing because only results for POM0 suggest that relocation may have a negative effect on abundance (Table 19; Fig. 10). Credit values for H_T

indicate a stronger erosion of genetic variation in scenario 4 compared to scenario 2, suggesting that Blackjack Crossing has a higher conservation value for genetic diversity (Fig. 11).

Table 19. Landscape Service Years (LSY) for adult abundance (N) and total expected heterozygosity (H_T) for four management scenarios under three best parameterizations remaining after shortPOM.

	debit		credit			
	Single Large	Multi- Small	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Adult abundance (N)						
POM0	3.503*	4.937*	-0.159	-0.776†	-0.158	-0.922‡
POM1	3.091*	5.256*	0.372	-0.561	-0.335	-1.285
POM2	3.636*	5.159*	-0.153	-0.969‡	-0.028	-1.228
Total expected heterozygosity (H_T)						
POM0	0.020*	0.020*	-0.008†	-0.006‡	-0.018*	-0.019*
POM1	0.020*	0.024*	-0.009†	-0.010‡	-0.023*	-0.023*
POM2	0.024*	0.023*	-0.016*	-0.012*	-0.023*	-0.022*

* $p < 0.0001$, ‡ $p < 0.01$, † $p < 0.05$

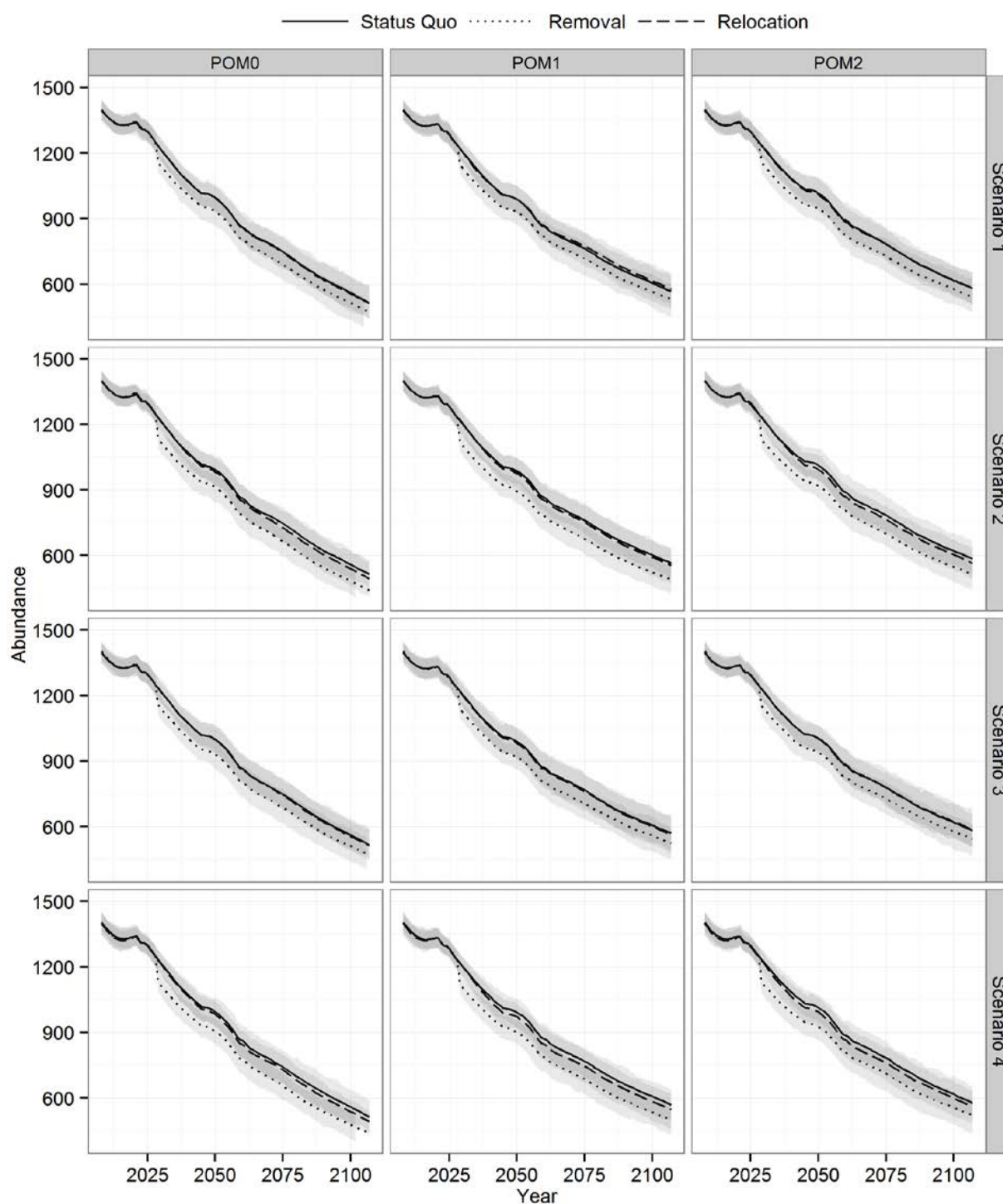


Figure 10. Adult abundance (N) over 100 years of the LEA simulation, for three parameterizations and four management scenarios. Separate lines are shown for status quo, removal, and relocation landscapes.

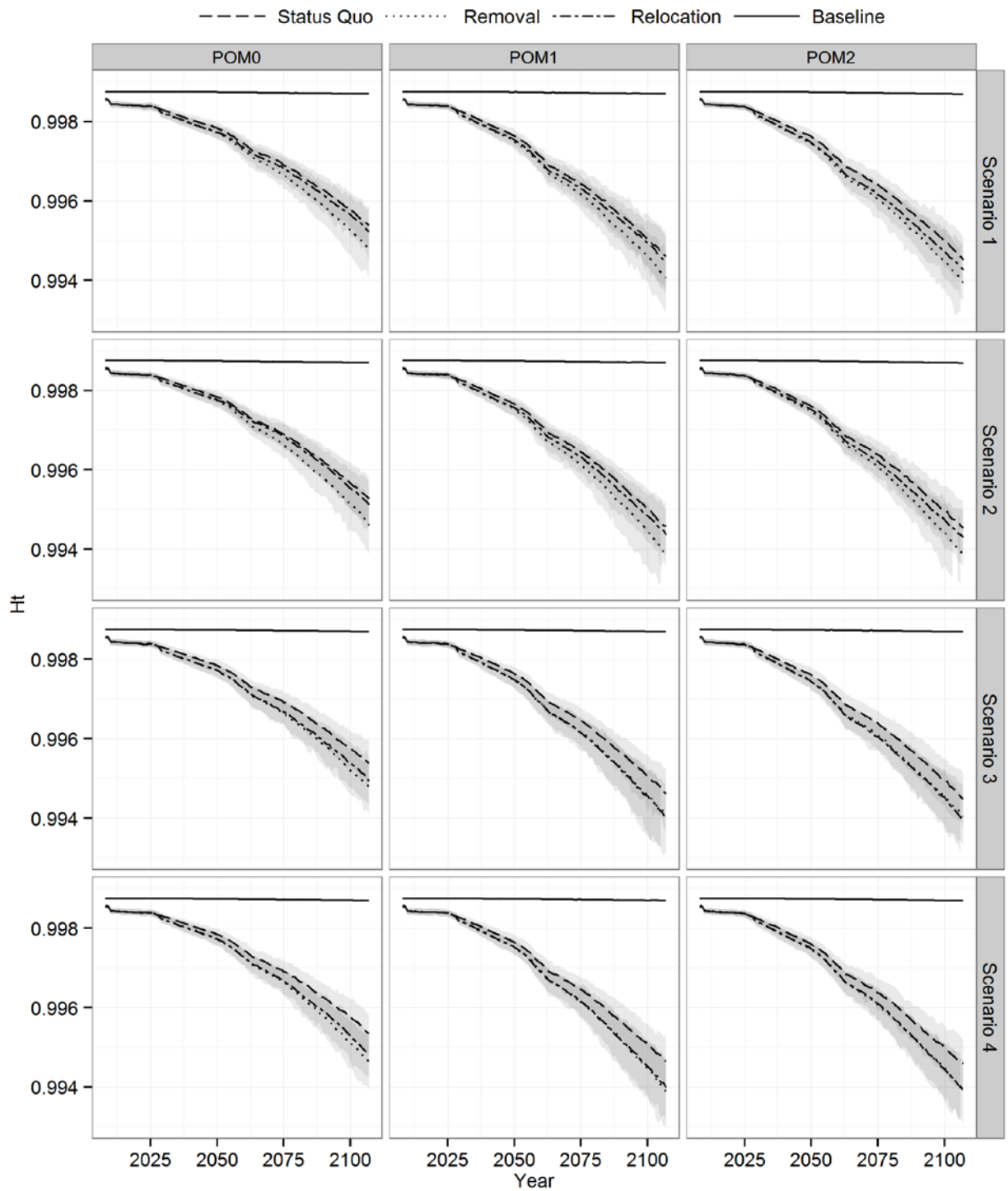


Figure 11. Total expected heterozygosity (H_T) over 100 years of the LEA simulation, for three parameterizations and four management scenarios. Separate lines are shown for status quo, removal, relocation, and baseline landscapes.

6.2.5 Application of Decision Analysis

Decision Analysis was applied to determine if the range of uncertainty included across our three dispersal hypotheses affects the preferred decision for each service. Decision Analysis provides a structured approach for incorporating the role of uncertainty during decision making (Clemen and Reilly 2001). For brevity, Decision Analysis was applied to only credit values. The EV of a scenario given uncertainty in dispersal behaviors captured by the three parameterizations [or models] is estimated as:

$$EV[Scenario|Model] = \sum_{Model=1}^3 P[Model] * LSY_{Model,Scenario}$$

Where, Model is the index for the three uncertain parameterizations, P[Model] is the prior probability that a parameterization is true, and $LSY_{Model,Scenario}$ is the number of LSY credits generated by each scenario under a model. We assumed that each model has an equal probability of being true, $P[Model]=0.33$. The preferred scenario to minimize impacts on abundance was scenario 1, and scenario 2 was preferred to minimize the erosion of genetic variation (Table 20). Weighting the importance of abundance versus genetic variation when choosing among scenarios is ultimately a regulatory decision, but LEA provides a structured approach for making these decisions.

Next to apply Decision Analysis, we wish to know the expected LSY assuming that the best scenario is chosen given the expectations under each model. This value equals the EV of knowing the true dispersal behaviors (i.e., the true model) given the possible scenarios available:

$$EV[Model|Scenario] = \sum_{Model=1}^3 P[Model] * \max(LSY_{Model,Scenario})$$

Where, $\max(LSY_{Model,Scenario})$ is the largest number of LSY from the four possible scenarios for each parameterization. If $EV[Model|Choice]$ does not equal $EV[Choice|Model]$ for all parameterizations, then at least one of the three models indicates that a greater conservation benefit can be achieved by making a different choice than suggested when considering all models to be equally likely.

The expected value of learning the true mating system and emigration behaviors can now be estimated as the expected value of perfect information ($EVPI = EV[Model|Choice] - EV[Choice_p|Model]$). If EVPI does not equal zero then reducing uncertainty may lead to a different management scenario that provides greater conservation benefits.

For abundance credits the EVPI was 0.0418 LSY, indicating that the three parameterizations disagree regarding which scenario would provide the biggest benefit for abundance. For genetic credits, parameterizations disagreed regarding which scenario would minimize the erosion of genetic variation, which gave an EVPI of 0.00045 LSY. These EVPI values can be used to calculate a cost-effective level of investment in research into the mating system and emigration behaviors, as $EVPI * \text{price} / \text{LSY}$. LEA organizes habitat allocation decisions based on the in-kind replacement costs of the ecological services. Replacement costs of ecological

services for GT have not yet been derived for ACUB properties, which would be the cost to acquire and manage the property for tortoises plus the cost to perform the relocations.

Table 20. Results of Decision Analysis for the ecological services included in LEA. Expected Value (EV) across the three uncertain mating system and emigration parameterizations remaining after shortPOM, is expressed in Landscape Service Years (LSY).

Adult Abundance (N)		Total Expected Heterozygosity (H_T)	
EV Scenario uncertainty in models		EV Scenario uncertainty in models	
Scenario 1	0.0202	-0.0110	
Scenario 2	-0.77	-0.0094	
Scenario 3	-0.17	-0.0212	
Scenario 4	-1.15	-0.0213	
	EV True model scenarios		EV True model scenarios
	0.0620	0.0418	-0.00898
			0.00045

6.3 Conclusion

LEA indicated that GT are more sensitive to habitat fragmentation than habitat loss; therefore, it will be easier to mitigate single large habitat removal than many small impacts. While these are conclusions based on a simulation and not direct empirical evidence of fragmentation effects, which to the best of our knowledge currently don't exist, the IB-SEPM was based on as much empirical data on natural history traits as could be found in the primary literature (Appendix C). Further, the ability of the IB-SEPM to replicate realistic patterns in nature was then tested against empirical data using POM. As highlighted by the application of POM to GT, much remains to be learned about GT natural history. However, this study should raise concern regarding the influence of habitat fragmentation on GT and provides further evidence against Fahrig's (2003) argument that fragmentation has little to no effect on biodiversity independent of habitat loss.

POM0 led to the most consistent negative outcome for abundance, and as discussed in the chapter on POM, this parameterization assumes that male juvenile tortoises do not emigrate. LEA results for H_T indicate that relocating tortoises to Blackjack Crossing would help minimize the influence of drift and inbreeding compared to Brown Springs Young Rd. While Brown Springs Young Rd is directly adjacent to FB, Blackjack Crossing is much bigger and likely leads to retention of genetic variation due to the availability of more habitat (i.e., fewer emigrants are lost to areas with poor habitat quality). The approach offered here could also be used to evaluate relocation strategies intended to offset the erosion of genetic variation, which do not include any habitat loss. For example, given the availability of tortoises that were inappropriately removed from outside areas (i.e., waifs), what would be the genetic benefit of

introducing them in FB? Or, given the small GT populations outside of FB in the Chattahoochee Fall Line, what would be the genetic benefit of moving tortoises from FB into these other populations?

It is also interesting to note that while all relocations met with our interpretation of the State of Florida guidelines and impacted the same habitat area, important differences in the conservation value of these decisions were found. This highlights the ability of LEA to capture landscape-scale effects of management decisions (i.e., site-based metrics will often ignore landscape dynamics; Bruggeman et al. 2005).

Decision Analysis indicated that the management scenario that provided the greatest benefit for abundance was not the same scenario that minimized the erosion of genetic variation. Multiple small removals with relocation to Blackjack Crossing minimized erosion of genetic diversity. Therefore, habitat removals and relocations that approximate “habitat defragmentation” may be best for the retention of genetic diversity. This highlights the importance of including multiple services in habitat allocation decisions. Decision Analysis also indicated a financial benefit for further reducing uncertainty regarding the mating system and emigration behaviors prior to making habitat allocation decisions for the GT. We believe the POM/LEA techniques will provide valuable tools for assembling knowledge of GT natural history while weighing alternative management decisions.

7.0 Conclusions and Implications for Future Research/Implementation

Only by confronting models used for planning with observed data can we gain increased confidence in our management decisions. POM provides a structured approach for incorporating observed data into IB-SEPMs to test alternative hypotheses regarding how landscape patterns affect population processes. Forcing such models to confront reality is a critical step in the development of ecological theory (Grimm and Railsback 2005). However, model development for IB-SEPMs is more challenging than statistical models such as regression equations, due to the high dimensionality and stochasticity that characterize IB-SEPMs. The complexity of IB-SEPMs does provide the critical benefit of being able to simulate multiple patterns simultaneously. POM uses this increased realism to evaluate the ability of IB-SEPMs to approximate multiple patterns simultaneously. The ability of the model to generate multiple patterns permits a greater diversity of hypothesis testing and provides strict limits on the model's performance (Grimm and Railsback 2005). In this study, we were able to develop a comparative statistical framework to assess both parameter and structural uncertainty to assess the fit for IB-SEPMs for two very different species using a variety of data sources.

Importantly, results for RCWs indicated that connectivity data derived from the long-term bird banding program on CL were the most powerful for estimating dispersal behaviors (Table 4). And the benefit of those data was observed in the application of LEA to RCWs, which indicated that all accepted models agreed regarding which habitat allocation would provide the biggest benefit for abundance. Results also indicated less detailed data collected by conservation partners (i.e., HS) did help constrain parameter state space for RCWs (Table 4). Further, POM provided statistical evidence for data quality issues suspected at CNF (Table 3). Therefore, POM provided a valuable tool for including data from across various spatial scales, regardless of where fence lines are located, and assessing data quality. However, the dispersal models accepted by POM disagreed regarding which habitat allocation would minimize habitat fragmentation effects, estimated by increased erosion of genetic variation within breeding groups and greater accrual of genetic differences among breeding groups. Whether the remaining uncertainty for RCWs can be reduced by including results of recent radio telemetry work on juvenile females at Ft. Bragg (Moody et al. 2011), and therefore agreement on how to pursue EP to minimize habitat fragmentation, remains to be seen. However, the benefit of IB-SEPMs is the ease with which new hypotheses regarding biological processes can be included. An empirical genetic study in the Onslow Bight could help address this dispersal uncertainty, as well. Thanks to long-term bird banding and pedigree analysis we have a decent understanding of inbreeding depression in RCWs (Daniels and Walters 2000) but we lack the empirical genetic data in the Onslow Bight to know whether it poses a risk there.

The application of the POM framework provides many useful analyses. For example, had we been able to detect a significant relationship between remotely sensed data and group size then we could contrast prediction errors that result when different reproduction models are used. We still feel the use of remotely sensed data to predict fledglings has promise. However, the difficulties we experienced highlights the importance of establishing universal monitoring

techniques at broad spatial scales so that broadly available data provided by remote sensing can be related to a large enough sample size.

Use of POM to construct and test the GT IB-SEPM permitted an evaluation of the natural history traits critical for species persistence. Home range assignment rules had the biggest impact on the reproductive ability of simulated populations and on the model's ability to approximate monitoring data collected in the field (Tables 15 & 17). Therefore, radio telemetry data will likely continue to be critical for understanding natural history traits. We also found that, of the summary statistics evaluated, only Bur O-ring and F # burrows provide evidence for some data redundancy (Table 16). Therefore, we should begin finding ways to collect a greater diversity of GT monitoring data as there are likely more components of population structure that would help us understand life history traits. For example, while monitoring data on juveniles is exceedingly scarce, our application of new techniques in landscape genetics suggests that their behavior may contribute critically to retention of genetic diversity (Table 18, Figures 6 & 7). Development of monitoring techniques to understand the behavior of juvenile tortoises may be critical. Further, understanding interactions between habitat quality, the mating system, and emigration behaviors would also contribute critically to conservation planning. Knowledge gaps for the GT remain large because of their secretive life histories. We believe the habitat model, IB-SEPM, and POM analysis developed here can contribute to integrating field data with alternative hypotheses of natural history strategies that would be difficult to observe in the field.

The technologies developed here for the GT could be extended to other field sites. For example, building a database of burrow survey results and estimating habitat models for these same areas, as we have illustrated that habitat models can be constructed using nationally available data (Kowal et al. In press), would be a huge step forward in further evaluating whether GT's are more sensitive to habitat loss or fragmentation. Though we have provided evidence using the IB-SEPM, which was developed and tested using a variety of empirical data, of greater sensitivity of GT populations to habitat fragmentation, a database of more direct evidence would be useful. Another critical knowledge gap is linking molecular estimates of inbreeding with reduced survival of hatchlings.

Application of LEA to the GT indicated that the population on FB is expected to continue to decline due to nest predation. We used a nest predation rate derived from the primary literature, but this value likely varies greatly by site. An estimate of nest predation rates from FB would be helpful. While Decision Analysis indicated that we do not understand GT natural history sufficiently to prioritize the scenarios considered, it did indicate that Blackjack Crossing will likely contribute more to abundance and retention of genetic variation than Brown Springs Young Rd. The best strategy for GT management may be to implement habitat and relocation strategies that mimic habitat defragmentation, as observed under Scenario 2. We were able to more confidently prioritize habitat allocations for the RCW than GT due to the longer history of monitoring data collect for RCWs.

One interpretation of our results might be that given the existing level of uncertainty regarding GT natural history, that management decisions should be based on habitat values alone rather than use this IB-SEPM. In the absence of an IB-SEPM or a habitat model, Guyer et al. (2012) proposed a statistic to inform management. Based on surveys from across the species range, Guyer et al. (2012) suggested that below a critical GT density of 0.4 tortoise/hectare, reproduction is impaired. However, above 0.4 tortoise/hectare GT's were observed to adjust home range size to maintain social interactions. Below this critical density GT's restricted their home range size and social interactions to a few neighbors close by, but results also indicated that regardless of density, distance of dispersal events outside of their home range increased. The implication here is that populations below this density are thought destined for extinction unless some conservation intervention is implemented.

To evaluate how well our habitat model might predict GT density across FB, and thus extinction, we sampled FB using 600 m grid cells and contrasted tortoise density observed in the J Carter 2008-2010 burrow survey with our estimated global habitat model, which is our best estimate of current habitat conditions. Ordinary Least Squares regression was applied to quantify the relationship between GT density and habitat values (Fig. 12). We find a positive relationship but not a really strong correlation ($R^2=0.395$, $p<0.0001$). Therefore, factors other than habitat quality are impacting tortoise densities. For example, many areas have very high habitat quality but low tortoise density, and some have high tortoise density and low habitat value. Factors likely to contribute to variation between tortoise density and habitat values include nest predation, tortoise social interactions, patterns of dispersal, and land use history. These factors have all been included in the IB-SEPM we constructed in this study. Therefore, we don't recommend using the habitat model to predict tortoise density thresholds across the landscape, but hope that an IB-SEPM would be used for management instead.

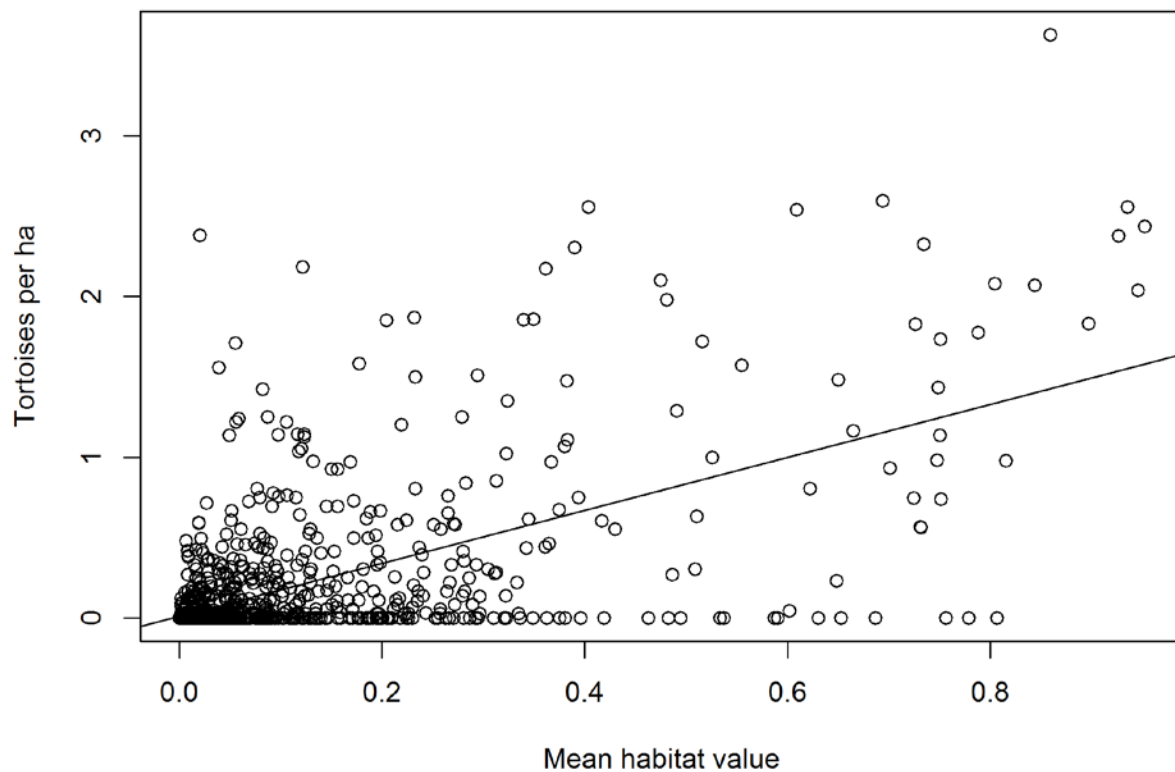


Figure 12. Relationship between habitat values from the global model and tortoise density ($n=1302$, $R^2=0.395$, $p<0.0001$, $y = 0.0033 + 0.458x$). Estimated by applying a 0.278 tortoises / burrow conversion factor to results from J Carter survey in 600 m grid cells sampled across FB. Conversion factor was derived from Ft Benning crew survey of HMU1 in which burrow occupancy was recorded.

Implementation of POM/LEA for Adaptive Management of habitat allocations for at-risk species is possible at the installation level. This may require a shift of natural resource management culture such that the ultimate fate of monitoring data would not be an Access or GIS database but an IB-SEPM. We can make POM accessible through the web using cloud resources to run a large number of alternative parameterizations. However, we would have to develop the interfaces between existing databases and POM so that data can be input and evaluated in seamless manner. Currently, adapting POM to various types of monitoring data (and formats) takes a considerable amount of time. For the GT this is eased by the earlier stages of monitoring data (i.e., there are few data and formats are relatively simple). In two projects outside of this SERDP work we have applied POM/LEA to support Biological Assessments for the RCW at CL and FB. As a deliverable for those projects we provided “LEA Viewer” software so that simulation results of the management scenarios could be viewed in a customized GIS viewer with supporting tables and figures. The LEA Viewer could also be migrated to the web. The vision would be to upload monitoring data as it is acquired to ensure continued data

quality. As data are acquired, installation personnel could run POM to test hypotheses regarding dispersal, for example. For RCWs once bird banding data are updated, the new dispersal patterns included in POM then could eliminate a larger number of possible dispersal parameterizations. The same could be true for new burrow surveys for GT. Then, when there is a need to change habitat allocations, personnel could use the best accepted parameterizations to estimate LEA debits & credits.

There are, however, limitations of the approaches developed here. The first is the amount of time required to develop a custom IB-SEPM for a single species. While we were able to adopt the RCW model from the literature (Bruggeman et al. 2009 was based on Letcher et al. 1998), we had to build the GT IB-SEPM from scratch. Constructing the model, including the development of a habitat model, new landscape genetic techniques, and application of LEA and POM required roughly two-years of work. We have been able to apply LEA & POM for RCW's to new sites within as few as eight months. The time required will vary based on how much monitoring data is available and how many landscape scenarios are requested.

The benefit of developing a custom IB-SEPM is the ability to structure the code and model assumptions more closely to natural history traits. For GT's this allowed us to focus the mating system on spatial components of home range for both sexes. For RCWs, this permitted including the landscape dynamics of helpers in ecologically realistic ways. The second limitation is the amount of data required to characterize the influence of environmental heterogeneity on a species' mating system and dispersal behaviors. IB-SEPMs can be viewed as "data hungry", but these models do describe important interactions between species and their environment that can have big impacts on land use decisions. However, once these limitations are tackled, spatially- and temporally-explicit simulation models are available to test a variety of hypotheses about natural history and for evaluating management scenarios. Development of user friendly software, after the initial development of the IB-SEPM, would help overcome these limitations, but as discussed above would require changes in installation-level activities.

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APPENDIX A

DESCRIPTION OF THE INDIVIDUAL-BASED, SPATIALLY-EXPLICIT POPULATION MODEL FOR THE RED-COCKADED WOODPECKER

Details of the RCW IB-SEPM are described below following the Overview, Design concepts, and Details (ODD) protocol, which is intended to provide a standard approach for describing agent-based models across studies to increase transparency (Grimm et al. 2010).

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1. PURPOSE

The purpose of the Red-cockaded Woodpecker (RCW) IB-SEPM, originally described in Letcher et al. (1998) and updated here, is to model a complex social system that includes spatially restricted dispersal. The purpose of the model is two-fold. The first is to further understanding of how landscape patterns affect reproduction and dispersal behaviors by applying Pattern Oriented Modeling (POM). The second is to estimate how landscape change may affect population viability and use Landscape Equivalency Analysis (LEA) to estimate the conservation value of alternative landscape compositions (Bruggeman et al. 2005). The first approach is a retrospective analysis, using historical data to estimate model parameters through inverse modeling (Grimm et al. 2005). The second approach is a form of projection analysis of alternative management scenarios.

2. ENTITIES, STATE VARIABLES, AND SCALES

Breeding groups. The RCW IB-SEPM simulates the cooperative breeding system of RCWs. Breeding groups consist of male and female breeders, fledglings, and, helpers who are usually male and full or half-sibs to the fledglings (Figure A1; Walters et al. 1988). Male helpers play a critical role in population dynamics by participating in the defense of the territories, feeding of nestlings, and inheriting their natal territory upon the death of the male breeder. Male helpers will preferentially inherit their natal territory upon the death of the breeding male, out-competing floaters and helpers in adjacent territories [described further below]. In contrast, we are more uncertain of the role female helpers play, but review of bird banding data indicate they do not inherit their mother's role as a breeder in their natal territory – so this was excluded from the model. Floaters of both sexes are also present in the region, which move continuously seeking a breeding vacancy in a territory (Walters et al., 1988).

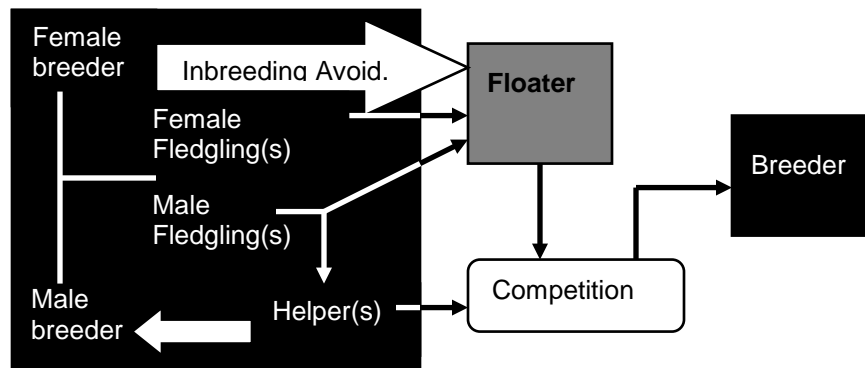


Figure A1. Breeding group structure and demographic transitions for the Red-cockaded Woodpecker. Black boxes denote breeding territories and the grey box denotes the matrix crossed during floating behaviors. Over 90% of time when a helper inherits his father's territory, his mother disperses to avoid inbreeding (Daniels and Walters, 2000).

Appendix A

Agents/individuals. The basic entity modeled is a bird. Each bird is characterized by its sex, age, status (i.e., fledgling, floater, helper, or breeder), current location, natal territory location, and alleles present at four genetic loci. If it is a floater, its dispersal direction, dispersal path, and number of steps available to be taken within a season are tracked. If it is a breeder, its breeding territory location and number of fledglings produced are tracked. If it is a potential competitor for a breeding vacancy (i.e., a helper or floater), the bird's perceptual distance is also tracked.

Spatial Units. Each cell is a 100 m x 100 m or 1 hectare. Territory centers are designated as a 1 hectare area and are based on GIS shape files provided by each stakeholder agency.

Landscape Classification. The population was simulated over an eight county area in coastal North Carolina covering an approximately one million hectare area, commonly referred to as the Onslow Bight Landscape. Landscape classification in the Onslow Bight was performed by Dr. Aaron Moody's lab at University of North Carolina. Dr. Moody's lab at UNC used FEMA Lidar data collected in 2001 and the National Land Cover Database to identify eight cover types including forested, pocosin, scrub, open, water, wetlands, and two classifications of RCW habitat (Table A1). RCW habitat was identified using Maxent (Phillips et al. 2004), which is a machine learning algorithm that uses presence data to identify localities with similar features. In our case, the presence data were forest metrics collected during ground surveys of RCW foraging habitat on MCBCL from 1999-2001. These plots were then classified by those meeting USFWS's recovery standard for habitat and those meeting the managed stability standard (USFWS 2003). The plots were then used to train Lidar data to identify remotely sensed attributes indicative of recovery standard and managed stability standard habitat. These attributes along with GAP data were incorporated into Maxent to identify areas across the Onslow Bight with environmental attributes close to the empirical mean observed at the presence sites. The Maxent model was able to capture 74% of active territories across the Onslow Bight and indicated that only 3.2% of the Onslow Bight meets the recovery standard for habitat (Figure A4).

Table A1. Description of the landcover types that constituted the landscape used in the simulation.

Description	Source
Forested, Pocosin, & RCW Habitat - Vegetation with a height ≥ 7 ft and a canopy cover (above 21ft) $\geq 5\%$	NLCD & Lidar
Open - Roads, Developed Areas, Agriculture, Pasture, vegetation with a height < 7 ft	NLCD & Lidar
Water	NLCD
Wetlands - Non-pocosin wetlands with a vegetation height < 7 ft	NLCD & Lidar

Time.

POM Approach. The simulation experiment was conducted from 1997 to 2009 because data describing the population, landscape and climatic conditions were all concurrently available during this time. Four seasonal time steps were simulated within each year, starting with Spring.

LEA Approach. The simulation experiment was conducted from 2009 to 2108. Four seasonal time steps were simulated within each year, starting with Spring. The seasons corresponded to the months listed below.

Weather Data. Weather data were included to support the reproduction submodel (described below in item 7). Climate data were assembled from 2 weather stations in Onslow County through the North Carolina State Climate Office (www.nc-climate.ncsu.edu) to characterize local climate conditions. These data date back to 1996 and no trend could be detected with temperature or precipitation.

We then summarized the data to correspond with the IB-SEPM's seasonal time step. Because productivity reflects the cumulative influence of environmental conditions on the energetics of birds prior to and including the season of reproduction, we used seasonal averages prior to the mating season (Summer: July, August, September; Fall: October, November, December; and Winter: January, February, March) and the season in which mating and fledging occurs (Spring: April, May, June). These seasonal averages were derived from monthly averages obtained from 2 weather stations in Onslow County through the North Carolina State Climate Office (www.nc-climate.ncsu.edu). Air temperature (F) and wind speed (mph) were collected from the New River Marine Corps Air Station (MCAS) AWOS – III weather station (station ID: KNCA). The monthly summed precipitation (inches) was collected from the COOP-TP weather station at Hoffman Forest (station ID: 314144),

Appendix A

because these data were not available at MCAS. Precipitation data were missing from the winter months in 2007, so we averaged precipitation in winter months across all other years to provide an estimate of precipitation in 2007.

POM Approach. Observed data from these weather stations were used to include the actual weather conditions that existing during the simulation period.

LEA Approach. A submodel to project future climate conditions by sampling from each seasonal distribution at random was included. One random sample is collected for each Monte Carlo iteration used. The climate submodel also allows us to include possible climate trends by changing the mean and variance of these distributions over time.

3. PROCESS OVERVIEW AND SCHEDULING

Pseudo-code describing the model scheduling is provided below and is largely based on Letcher et al. (1998).

<i>POM Approach</i>	<i>LEA Approach</i>
Read data files (parameter values, landscape, territory locations by year, initial population, observed patterns used for filtering) For parameterization p For monte carlo m Gene Drop CL 1986 to 1997 For year t=1997 to 2009 If t=0, Initialize with RCWs observed in 1997 Update available territories For season s If s=Spring Reproduction Add Immigrant Age birds Estimate genetic parameters [Nei] Population census End if Spring Mortality If s>Spring, Natal dispersal Competition Dispersal End season End t [year] End m Calculate summary statistics (negative log likelihood (-log[L])) End p	Read data files (parameter values, landscape, territory locations by year, initial population, shapefiles describe habitat loss and restoration) For parameterization p For monte carlo m For land L For year t=2009 to 2108 If t=0, Initialize with RCWs observed in 2009 Update available territories If L=mitigation & translocate=FALSE Add Mitigation territories for natural colonization For season s If s=Spring Reproduction Add Immigrant Age birds Estimate genetic parameters [Nei] Population census End if Spring Mortality If s>Spring, Natal dispersal If s=Fall & L=mitigation & translocate=TRUE Translocate birds Competition Dispersal End season End t [year] End L End m Randomization test for territory metrics Collect landscape-scale data for LEA End p

4. DESIGN CONCEPTS

The basic principles underlying this model's design are the associations between demographic and genetic components of population structure in a dynamic landscape. The design will allow us to understand how demographic and genetic properties relate in dynamic landscapes. Demographic stochasticity is included in the mortality, reproduction, competition, and dispersal submodels described below. The model includes five hypothetical genetic loci with different levels of allelic richness, further described below. Population genetic characteristics are summarized following the method of Nei (1973) coded directly within the simulation.

4a. POM APPROACH

Initially, SEPMs were criticized due to their complexity, large data requirements, and use of uncertain parameter estimates (Beissinger and Westphal 1998). However, an approach called Pattern Oriented Modeling (POM) has been used to construct and validate SEPMs with less data than previously imagined (Grimm et al. 2005; Wiegand et al. 2004). Pattern Oriented Modeling is used to determine the model's ability to replicate complex patterns observed in nature. Therefore, the model is designed to compare summary statistics from the simulation to summary statistic that characterized actual populations, or observed patterns.

We calculate the mean of multiple simulated runs to eliminate the internal model stochasticity, thereby treating the stochastic simulation model as deterministic on the level of the simulated summary statistics (Martínez et al. 2011). We estimate likelihood functions $L[S|O]$ to describe the deviation between the summary statistics of the patterns observed in the Onslow Bight (O) and the patterns generated by each dispersal parameterization (S) (Csillery et al. 2010; Wood 2010). Patterns generated by the IB-SEPM were collected in Spring (item 3) for the same time intervals and territories present in the observed patterns (Table A2). Averages for all simulated patterns were taken across the 200 Monte Carlo iterations for each dispersal parameterization. For count data, including PBGs, group size, and connectivity, a Poisson negative log likelihood was estimated. For example, the negative log likelihood ($-\log[L]$) for group size on CL was estimated as:

$$-\log(L\{S|O\}) = \sum_{t=1997}^{2009} \sum_{i=1}^{106} -\log\left(\frac{S_{ti}^{O_{ti}} e^{-S_{ti}}}{O_{ti}!}\right)$$

Where t =year and i =territory. The temporal and spatial extent of data included in the $-\log[L]$ estimates for connectivity, PBGs, and group size at other sites varied as described in Table A.2.

For genetic data, in which the observed data were generated by a gene drop iterated 10,000 times, a Gaussian distribution was assumed.

$$-\log(L\{\mu^S|\mu^O, \sigma^O\}) = \sum_{i=1}^{106} \sum_{j=1, i \neq j}^{106} -\log\left[\frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(\mu_{ij}^O - \mu_{ij}^S)^2}{2\sigma^2}}\right]$$

Appendix A

Where, μ^s equals the average D_{ij} across 50 Monte Carlo iterations and μ^0 and σ^0 equal the mean and standard deviation for D_{ij} from the 10,000 iterations of the observed gene drop. The same approach was applied to number of unique alleles per breeding group on CL, except it was summed across the vector describing unique alleles per territory rather than a territory by territory matrix.

The goal is then to minimize the deviation between the summary statistics of the observed and simulated patterns; i.e., the parameterization must be determined that minimizes the negative likelihood functions.

Table A2. Description of observed data available from each landowner and their associated temporal and spatial scale.

Observed Pattern	Camp Lejeune (CL)	Croatan National Forest (CNF)	Holly Shelter (HS)
PBG	1997 to 2009	1997 to 2001	NA
Group Size	1997 to 2009 Territories 1 to 106	1997 to 2001 Territories 203 to 392	2009 Territories 401 to 434
Connectivity	Territories 1 to 106	NA	NA
Minimum pair wise genetic distance - D_{ij}	Territories 1 to 106	NA	NA
Unique Alleles per breeding group - A_i	Territories 1 to 106	NA	NA

4b. LEA APPROACH

LEA is an extension of resource-based compensation applied to a landscape-scale (Bruggeman et al 2005). Resource-based compensation determines the amount of restoration required to equate an individual's well-being before loss of an ecological resource with their well-being after that loss (Jones and Pease 1997). A "service-to-service" approach is used wherein adequate compensation is made to the public if the habitats restored provide equivalent types and levels of ecological services as the habitats lost. Ecological functions can be treated as goods and services when a direct or indirect benefit to humans can be demonstrated (deGroot et al 2002). In this analysis we assume that the ecological services that provide these benefits are abundance and genetic variance (Loomis and White 1996; Bruggeman et al 2005). LEA estimates the equivalency of habitat patches traded in a

fragmented landscape based on changes in three ecological services, 1) abundance and genetic variance 2) within and 3) among local populations, measured at the landscape-scale.

The spatial apportionment of neutral genetic variance is included to ensure that trades do not move the **balance** between genetic drift, local extinction, and migration farther away from that observed under a “baseline” landscape. Neutral genetic variance is the variety of alleles present in the population that do not contribute to adaptive traits and whose fate is determined by genetic drift, gene flow, inbreeding, and local extinction (Manel et al 2003). Population genetic studies have shown that spatially subdivided populations benefit from migration rates that are high enough to episodically contribute to recruitment, thereby lowering rates of loss of genetic diversity and rates of inbreeding accrual, but low enough to maintain genetic differences among breeding groups to provide opportunities for adaptive evolution (Mills and Allendorf 1996; Wang 2004). However, the appropriate amount of migration required to offset genetic drift and inbreeding will vary based on an organism’s natural history and the degree of habitat loss and fragmentation at the landscape level (Lacy and Lindenmayer 1995; Daniels et al 2000).

Spatially subdivided populations in intact landscapes have demonstrated an ability to maintain genetic variance both within and among breeding groups while preventing inbreeding depression (reviewed in Bruggeman et al 2005). Therefore, LEA incorporates a “spatially-explicit” planning objective as the allocation of habitat yielding the spatial apportionment of neutral genetic variance observed prior to habitat loss and fragmentation (i.e., a baseline landscape) (Meffe 1996; Bruggeman et al 2005). The baseline landscape represents the spatial distribution of habitat in which rates of recruitment and migration achieve this balance. The conservation value of a LEA credit increases as habitat trades are able to move the balance between rates of recruitment and migration closer to levels observed prior to habitat loss and fragmentation, or a “baseline” apportionment of habitat. This reduces the probability that changes in recruitment and migration would lead to the expression of deleterious traits that result from mating between close relatives (inbreeding depression). Similarly, this reduces the probability that changes in migration would disrupt locally adapted gene complexes due to mating between individuals from different regions (outbreeding depression). In this way, LEA focuses on protecting the environmental context that permitted adaptive evolution, rather than attempting to identify all adaptive components of genetic variance (Moritz 2002).

5. INITIALIZATION / CONSTRAINING FACTORS

The initial bird list was constructed from monitoring data provided by each public landowner: Marine Corps Base Camp Lejeune (CL), Croatan National Forest (CNF), and Holly Shelter State Game Lands (HS).

5A. FIELD DATA COLLECTION

Camp Lejeune

Data from CL consisted of bird banding records from 1986 to 2009. During this time, all adults were banded with unique color band combinations and subsequently all nestlings and unbanded

immigrant adults have been similarly banded. Each year members of each group were identified from these color band combinations and the status of each group member (i.e., breeder, helper, floater) was ascertained. Active cavity trees were checked for the presence of a nest weekly, each nest discovered was then monitored and the number of young fledged from each was determined. The result is a complete census and determination of reproductive success for the entire population each year. See Walters et al. (1988) and Walters (2004) for a complete description of census and reproductive monitoring methods.

Croatan National Forest

The CNF RCW monitoring program was initialized in 1989 using the same techniques as CL's, however, due to funding and administrative difference between the agencies, the CNF records did not report consistent observations of social group composition after 1997. Therefore, data from 1997 were used to estimate the location of adults in 1997 to initialize the model. The dataset did distinguish between adults and fledglings for each territory from 1997 to 2001, and these demographic patterns were cautiously included into POM.

Holly Shelter

Data from HS consisted of nest check records, reporting whether a pair attempted nesting from 1994-2008. In order to collect more detailed data similar to other properties, a field crew from the Conservation Management Institute at Virginia Tech, under the direction of Ken Convery monitored the number of adults and fledglings at Holly Shelter. The crew visited known territories from May-July at sunrise and at sunset when the birds enter or emerge from their roosts. Nest cavity trees were identified by investigating each identified cavity tree with a video probe attached to a telescoping pole that could be placed within the cavity. Once the nesting cavity for each group was found, status updates were collected every 7-10 days until nest outcome (i.e., # fledglings) was determined.

5B. POM APPROACH FOR INTEGRATING FIELD DATA

The POM analysis begins in 1997, so the CL bird banding records were then used to assemble the actual RCWs present on CL that year. The banding records allowed us to calculate the age of all birds born on CL and to know their sex, status, and their current and past locations including natal and breeding territories. For birds of unknown age, sex, or location, which were floaters born outside of CL (immigrants), these attributes were assigned at random at the start of each Monte Carlo iteration. A random territory within CL was chosen as the starting point for the movement of floaters with no recorded location.

A total of 48 territories were active in 1997, and 214 birds were observed on CL, 13 of which were floaters. We were also able to construct a pedigree for the birds on CL. For each breeding event, we recorded the unique bird bands of the parents and all offspring. From 1986-2009, 888 breeding events were recorded. The pedigree was used to estimate the population genetic structure in 1997, based on a gene drop, which uses the principles of Mendelian inheritance to randomly select alleles from the parents for transmission to offspring. The gene drop is performed for breeding events

occurring between 1986-1997 at the start of each Monte Carlo iteration [see further description in Submodels].

We also included the provisioning of new habitat areas on CL, in which pine savannah was restored using fire and mechanized equipment and artificial cavities were constructed (Fig. A2). We included the new territories in the simulation the year they were made available in the field.

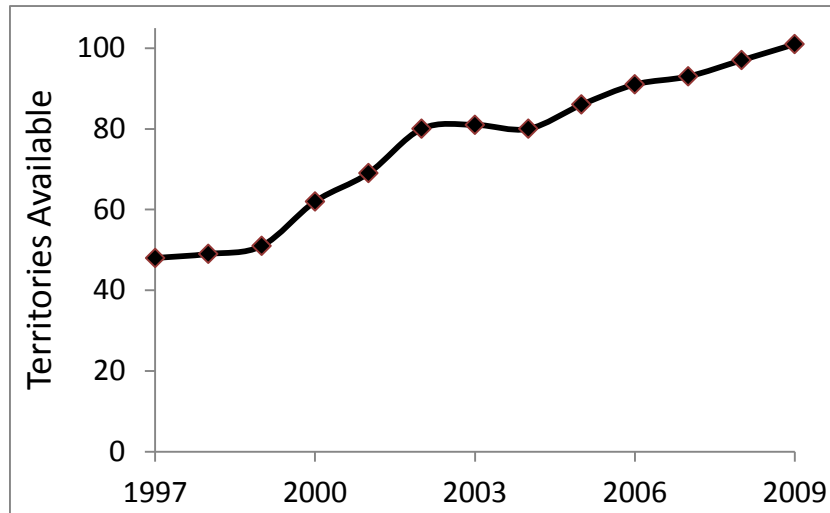


Figure A2. Number of territories available on Camp Lejeune based on their recovery plan.

For CNF, the bird banding records were used in the same manner as described for CL. However, there were more uncertain records. Therefore, if two adults of unknown sex were recorded, we assumed these were male and female breeders. If more than two adults were recorded of unknown status, we assumed two were breeders and the others were male helpers. The ID, age, and sex were assigned at the start of each Monte Carlo iteration. A total of 237 birds were present on CNF across 65 territories in 1997, 7 of which were floaters.

We were unable to assemble a pedigree for CNF. Therefore, we assumed all birds were unrelated, or founders, at the start of the simulation. Because the genetic structure on CNF was not used to estimate model fit, this lack of pedigree does not affect model results. However, the model did allow floaters from CNF to immigrate to CL, so these birds do require alleles.

For HS, the nest check records were used to determine the number and location of breeders in 1997. The ID, age, and sex of these birds were assigned at the start of each Monte Carlo iteration. For those breeding pairs reported as having attempted nesting, we assumed an 80% probability of producing fledglings, based on equation 2, which estimates the probability of nest success, in Letcher et al. (1998). At the start of each Monte Carlo iteration, breeding success was estimated and the number of fledglings produced was determined by pulling a random number from a Poisson distribution between 1 and 4, as no more than four fledglings have ever been reported for RCWs in the study area. No monitoring data on floaters or helpers was available at HS. For helpers, we allowed the model to assign helpers to territories in 1998 based on fledgling success in 1997. Floaters were

added to HS based on the ratio of active territories to the number of floaters observed on CL (13/48 = 0.27). In 1997, HS contained 28 active territories, 56 breeders, and eight floaters.

We were unable to assemble a pedigree for HS. Therefore, we assumed all birds were unrelated, or founders, at the start of the simulation. Because the genetic structure on HS was not used to estimate model fit, this lack of pedigree does not affect model results. However, the model did allow floaters from HS to immigrate to CL, so these birds do require alleles.

5C. LEA APPROACH FOR INTEGRATING FIELD DATA

To contrast RCW population viability across different land use scenarios, multiple landscapes were developed. Below, we describe how empirical data were incorporated into each of the landscape treatments.

Recovery Landscape

Monitoring data at CL were used to initialize the MCBCL population with the actual age, sex, territory location, and status of birds observed in 2009. However, birds at territories 37, 50, and 70 were treated as floaters in the 2009 population as those clusters had already been removed from territory point file provided by MCBCL to reflect past consultations with the USFWS. The age of birds not banded as fledglings remained unknown, so age was randomly assigned at the start of each Monte Carlo simulation by choosing from a normal distribution with a mean of 4 and standard deviation of 1.

Monitoring data at CNF were collected by a new field crew in 2009. While they were able to visit all territories that had been active in the previous year, they did not have time for multiple visits needed to enumerate helpers. Review of their historical data indicated 0.47 helpers per PBG. Therefore at the start of each Monte Carlo simulation 1 helper was added to each PBG on CNF with a 0.47 probability. Also, the age of birds could not be determined on CNF, therefore at the start of each Monte Carlo simulation the age of adults was chosen from a normal distribution with a mean of 4 and standard deviation of 1. Also, floaters were not counted on CNF and historical records indicated a low incidence of floaters, likely due to low sampling effort. Therefore, we did not initialize CNF with any floaters and let the simulation introduce them over time. Floaters have the highest mortality rate so their absence in the first year should not have an appreciable effect.

Monitoring data at HS were collected by field crew from the Conservation Management Institute at Virginia Tech under contract to MSU in support of our SERDP contract (SI-1656). All known cavity trees were visited multiple times from May-July at sunrise and sunset to estimate number of breeders, helpers, and fledglings. No floaters were counted as they were not part of the scope of work, therefore we did not initialize HS with floaters and let the simulation introduce them over time. Age was randomly assigned at the start of each Monte Carlo simulation by choosing from a normal distribution with a mean of 4 and standard deviation of 1.

All birds were assigned alleles at five hypothetical genetic loci. The first allele assumed that every founding individual is heterozygous and contains two unique alleles (i.e., total alleles = 2 x number of breeders in the founding population, an Infinite Alleles Model (IAM) of genetic variation). In ad-

dition, we added 4 more loci with lower levels of allelic richness to parallel levels of genetic diversity observed in nature. Fike et al. (2009) found that the number of microsatellite alleles per loci in RCWs ranged from 2 to 5, so we included four loci that sampled alleles from a normal distribution with standard deviations including 0.05, 0.25, 0.5, and 1.0, allowing us to approximate observed levels of allelic richness.

Table A3. Initial population used for the Recovery simulation

	Active	PBGs	Helpers ¹	Fledglings	Floater ²	Total
MCBCL	82	79	60	122	30	373
CNF	54	53	0	103	0	210
HS	34	34	27	54	0	149
Total	170	166	87	279	30	732

¹Helpers were not counted at CNF in 2009

²Floater are only opportunistically monitored at MCBCL and not monitored at CNF and HS

Landscape Dynamics: Recovery planning

The simulation is temporally explicit so data regarding when and where clusters will be added to achieve recovery were needed. MCBCL had a well specified recovery plan, which was described in the “Lej_Active_Partition_Dates.shp” file sent in November of 2009 as part of our SERDP effort. This file includes locations for 189 clusters and anticipates restoring the last cluster in 2057 (Figure A3). HS is not required to restore additional habitat to contribute to recovery. We included the territories found to be active in 2009 (i.e., 34 PBGs), plus four territories included in the “Lejeune_Off_Base_Partitions.shp” that are believed to be available for birds currently. The four additional active clusters have the following IDs (first HS’s ID then MCBCL’s ID): CH2 (HS13), MRC (HS25), MTI (HS6), and WHC (HS31).

As part of our SERDP contract we helped CNF devise a new recovery plan. Clusters were prioritized for restoration based on four factors: 1) density of active clusters within 1.5 km; 2) burn frequency, which was used as an indicator of operability; 3) Euclidean distance to the nearest cluster; and 4) habitat potential. Habitat potential was estimated using a regression model that estimated group size, or number of adult birds, using Lidar-derived characteristics as the independent variables. CNF plans to allocate a total of 174 territories by 2086 to meet their recovery goal (Figure A3).

Appendix A



Figure A3. Recovery plan for the Onslow Bight landscape for MCBCL and CNF. HS is already at their required recovery contribution of 38 territories.

Appendix A

The recovery landscape was based on the landscape classification in the Onslow Bight (described in Section 2).

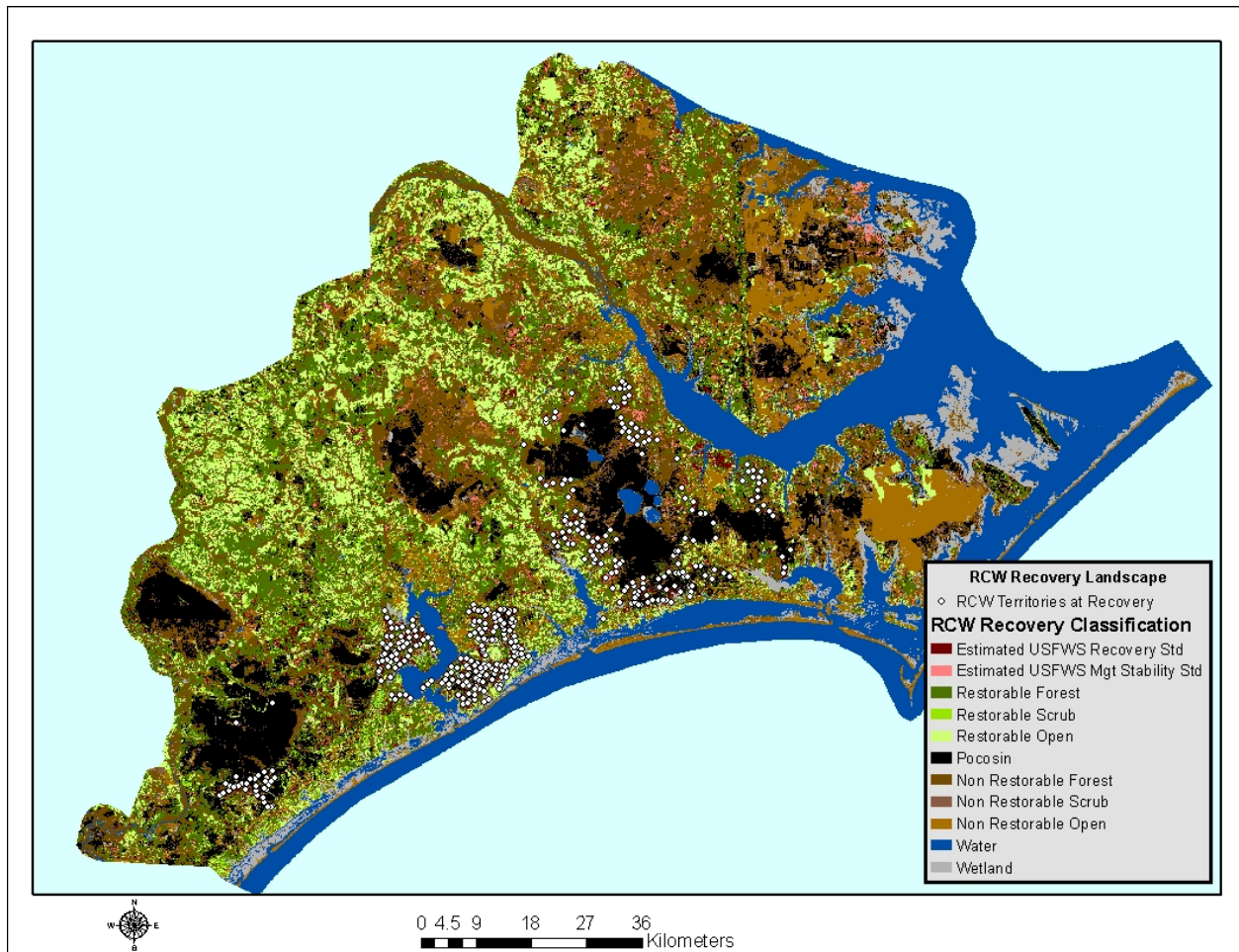


Figure A4. Recovery landscape classification generated under SERDP SI-1656. 401 RCW territories are allocated to achieve recovery.

Mitigation Landscape

The mitigation landscape was simulated by first simulating the Recovery landscape, and then making clusters available outside of Main Base. MCBCL performed habitat analysis to determine the number of clusters as well as estimated date of availability for off-base clusters (Table A4).

Table A4. Estimated time when new clusters outside of Main Base will be added.

	Stones Creek	Shaken Creek	Bear Garden	Oak Island	Hoffman Block 10	Sleepy Creek	GSRA
2010-2020	2	6	3	0	0	0	3
2021-2030	2	3	0	0	2	0	7
2031-2040	3	1	2	0	0	0	35
2041-2050	4	0	8	6	9	0	11
2051-2060	2	0	15	0	4	0	5
2061-2070	0	0	17	0	9	2	0
2071-2080	0	0	0	10	0	0	0

Pre-settlement / Baseline Landscape

The baseline landscape was used to estimate the spatial apportionment of genetic variation observed prior to habitat loss and fragmentation. Therefore, a pre-settlement estimate of vegetative composition was used (Frost and Costanza 2007). Frost and Costanza (2007) compiled county soil series and then estimated historic vegetative composition from soils data. We identified areas suitable for RCWs as those thought to historically contain Longleaf or mixed pine savannah. We estimate 479,083 hectares of the Onslow Bight (48%) likely served as RCW habitat historically.

To allocate habitat across the pre-settlement landscape, we first completed a review home range studies. We define home range as the area used for breeding and foraging, but all of the foraging habitat is not necessarily defended against other RCW groups. Twenty-one studies were identified. The majority of home range studies used the Minimum Convex Polygon (MCP) method to calculate home range, but many have argued that the Fixed Kernel method is a more accurate estimate of RCW habitat (Convery 2002; Franzreb 2006; Wood 2008). The Fixed Kernel method uses a probabilistic approach to determine home range size based on the density of RCW observations made while following birds during foraging. Home range tends to decrease during nesting season when adults forage closer to the nest. We felt the best estimates for home range size in a pre-settlement landscape were those obtained outside of the nesting season and using a Fixed Kernel method (i.e., Convery 2002; Walters et al. 2002; Franzreb 2006). The mean home range size across these studies was 73 ha (min = 56; max = 128). Two of the studies reported a standard deviation of 5 hectares.

Therefore, we created a GIS toolbox that randomly assigns RCW territories to the pre-settlement landscape by choosing a territory center at least 400 m from the nearest neighboring cluster. The distance criterion is based on a USFWS RCW management standard (USFWS 2003). Then the habitat area for each territory was randomly selected from a normal distribution (mean = 73 and standard deviation = 5). To accept a randomly placed cluster, there had to be enough RCW habitat within 800 m (James et al. 2001) of the territory center to make up the home range size selected. This method allowed for overlapping home ranges at a density approximating those currently observed. The average minimum distance among territories on Camp Lejeune is 625 m and for Holly Shelter and Croatan combined is 1,050 m. Based on one random selection process, we found that 3,998 territory centers fit into the pre-settlement landscape with an average minimum distance of 1,140 m among territories (Figure A5).

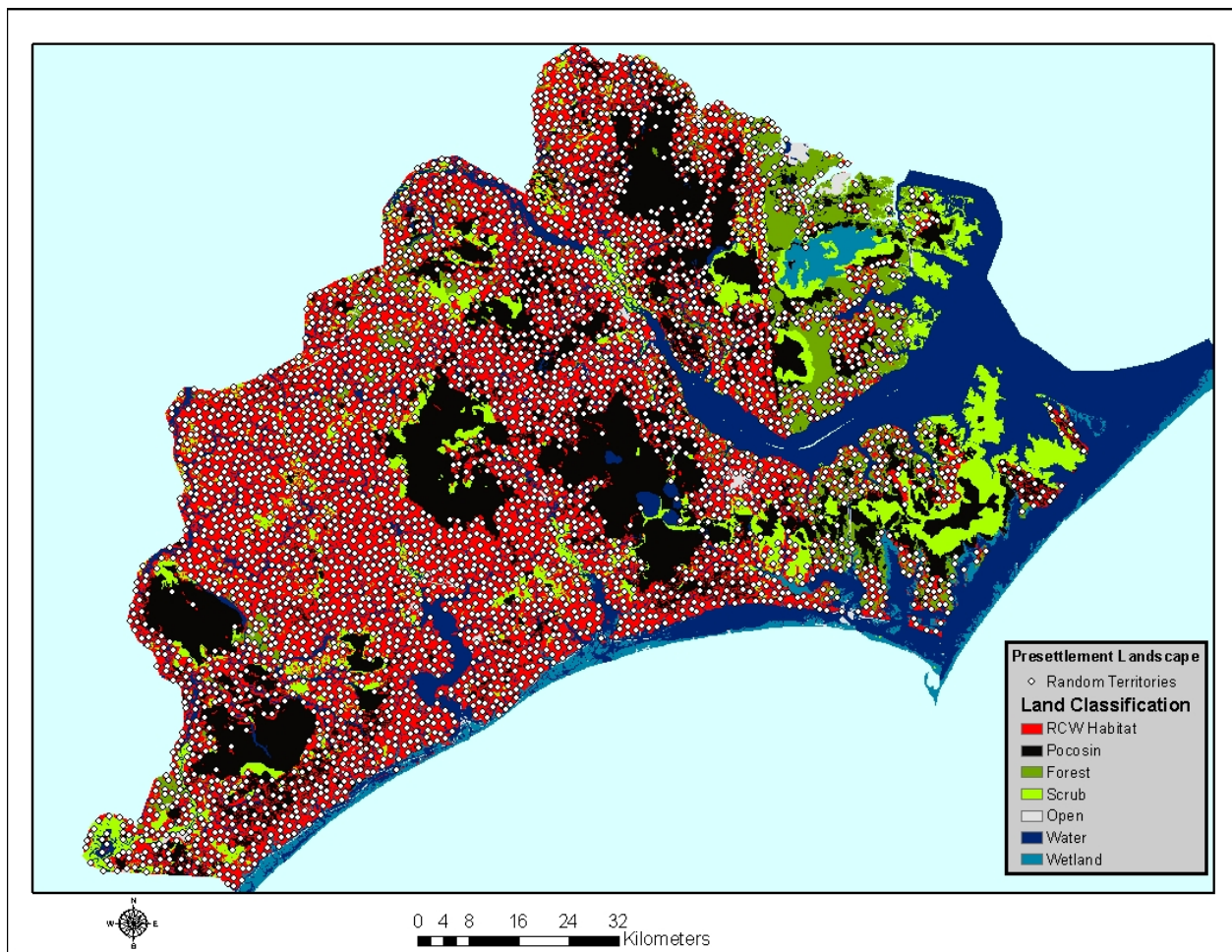


Figure A5. Baseline Landscape: one realization of the possible pre-settlement distribution of RCW territories in the Onslow Bight. 3,998 territories are displayed.

At the start of Baseline simulation, 80% of clusters were selected at random and given a breeding pair. Of these, 50% were randomly chosen to have one male helper. Age was also randomly assigned at the start of each Monte Carlo simulation by choosing from a normal distribution with a mean of 4 and standard deviation of 1.

6. INPUT DATA / OBSERVED PATTERNS

6A. POM APPROACH: OBSERVED PATTERNS

Each public landowner maintains an independent bird monitoring program. The detail, consistency, and time interval of data varied across landowners.

Camp Lejeune

The bird banding records from CL, described above, were used to summarize five different patterns. Potential Breeding Groups (PBG), defined as a male and female breeder with or without fledglings, serve as the regulatory benchmark for RCW Recovery (USFWS 2003). We tested the ability of different parameterizations to reproduce the time series of PBG observed on CL from 1997 to 2009 (Table A2). Group size, defined as the number of breeding adults and helpers in a territory, observed at each territory and each year was also used as a pattern.

Connectivity of territories was used as the third pattern. Connectivity was defined as the number of individuals born at location i that became a breeder in location j . These values were enumerated from 1997 to 2009. Territories on CL were numbered from 1 to 106. Therefore, the connectivity information was summarized as a 106×106 square matrices for males and females. For males, values along the diagonal represent the number of times a male helper inherited its natal territory, for example (Figure A1).

The last two patterns were population genetic patterns derived from applying a gene drop to the pedigree describing breeding events from 1986-2009, during which 888 breeding events were recorded. Individuals of unknown parentage or founders, which include birds not banded as nestlings, were assigned alleles at five hypothetical genetic loci. The first allele assumed that every founding individual is heterozygous and contains two unique alleles (i.e., total alleles = $2 \times$ number of breeders in the founding population, an Infinite Alleles Model (IAM) of genetic variation). In addition, we added 4 more loci with lower levels of allelic richness to parallel levels of genetic diversity observed in nature. Fike et al. (2009) found that the number of microsatellite alleles per loci in RCWs ranged from 2 to 5, so we included four loci that sampled alleles from a normal distribution with standard deviations including 0.05, 0.25, 0.5, and 1.0, allowing us to approximate observed levels of allelic richness.

The gene drop simulates the transmission of alleles from parents to offspring assuming Mendelian inheritance (i.e., their offspring had an equal probability of inheriting each of the two alleles). The gene drop was iterated 10,000 times from 1986 to 2009 to derive the observed population genetic structure in 2009. The mean and variance minimum pairwise genetic distance among breeding groups (D_{ij} , Nei, 1973) and number of alleles per breeding group were estimated from the gene drop for each of the five loci.

Croatan National Forest

As discussed under item 5, The CNF RCW monitoring program was initialized in 1989 using the same techniques as CL's, however, due to funding and administrative difference between the agencies, the CNF records did not report consistent observations of social group composition after 1997. Therefore, demographic patterns describing PBGs and group size were cautiously included into POM from 1997 to 2001.

Holly Shelter

As discussed under item 5, data from HS consisted of nest check records, reporting whether a pair attempted nesting from 1994-2008. However, we did not believe these data were recorded consistently enough to provide an estimate of PBGs over time. Therefore, we supplemented their field efforts in 2009 to obtain an estimate of the number of adults present at each territory. Therefore, the only observed pattern available was group size in 2009.

6B. LEA APPROACH: DISPERSAL PARAMETERS SELECTED FROM POM

Table A5. Dispersal parameters used to evaluate alternative landscape scenarios. The five models with the minimum $-\log[\text{Likelihood}]$ for demographic on HS and both demographic and connectivity patterns on CL were selected from POM. The dispersal parameters currently used in the RCW Decision Support System (DSS) were included for comparison.

	POM1	POM2	POM3	POM4	POM5	DSS
Foray distance of Female Helpers (# cells)	51	48	15	60	54	30
Foray distance of Female Floaters (# cells)	57	57	57	39	39	30
Foray distance of Male Helpers (# cells)	6	3	60	6	3	60
Foray distance of Male Floaters (# cells)	54	45	36	54	57	30
Female floater and Male natal dispersal speed (# cells)	7	18	20	18	20	6
Male floater dispersal speed (# cells)	18	19	15	18	19	12
Male Gap β Terrestrial	-0.00175	-0.00175	-0.00250	-0.00150	-0.00130	0
Male Gap β Water	-0.00300	-0.00500	-0.00100	-0.00375	-0.00150	0
Female Gap β Terrestrial	-0.00025	-0.00250	-0.00375	-0.00375	-0.00250	-0.00163
Female Gap β Water	-0.00425	-0.00075	-0.00350	-0.00275	-0.00480	-0.00163
Female Terrestrial Gap Sensitive Competition (0=off; 1=on)	0	0	0	0	0	1
Male Terrestrial Gap Sensitive Competition (0=off; 1=on)	1	0	1	1	0	0
Female Water Gap Sensitive Competition (0=off; 1=on)	1	1	0	1	1	1
Male Water Gap Sensitive Competition (0=off; 1=on)	0	0	0	1	1	0

7. SUBMODELS

Add Mitigation Territories (LEA Approach only [natural colonization])

Of the mitigation territories included in the simulation determine if there are at least 6 that can be made available for RCWs by the current year of the simulation that are within 3.2 km of a another possible recruitment cluster with another nearest neighbor within 3.2 km, which may or may not be already occupied by RCWs. If a minimum of 6 are found, add all mitigation territories to the list of available territories.

Gene drop (POM Approach only)

At the start of each Monte Carlo iteration, individuals of unknown parentage or founders, which include all birds on HS and CNF, and individuals on CL who were not banded as nestlings were assigned alleles at five hypothetical genetic loci. The first allele assumed that every founding individual is heterozygous and contains two unique alleles (i.e., total alleles = 2 x number of breeders in the founding population, an Infinite Alleles Model (IAM) of genetic variation). In addition, we added 4 more loci with lower levels of allelic richness to parallel levels of genetic diversity observed in nature. Fike et al. (2009) found that the number of microsatellite alleles per loci in RCWs ranged from 2 to 5, so we included four loci that sampled alleles from a normal distribution with standard deviations including 0.05, 0.25, 0.5, and 1.0, allowing us to approximate observed levels of allelic richness.

The gene drop is simulated for the years 1997 to 2009 for each parameterization and Monte Carlo iteration for all three public properties. The gene drop simulates the transmission of alleles from parents to offspring assuming Mendelian inheritance (i.e., their offspring had an equal probability of inheriting each of the two alleles).

However, for CL, a gene drop is also used during the Initialization process for each Monte Carlo iteration. Using a pedigree derived from bird banding data dating from 1986 to 1997, all founding individuals are identified. Then for the years 1986 to 1997 (i.e., the year the POM analysis begins), we simulate a gene drop through the actual breeding events that occurred. Therefore, the initial population on CL begins POM with gene correlations that reflects mating history, and therefore relatedness of family groups and individuals, from 1986 to 1997.

Aging

The age of each bird was incremented one year at the start of every spring. The maximum age recorded for RCW is 17 years (Conner et al., 2001), so birds were not allowed to live past this age.

Mortality

Class- and sex- specific mortality rates were derived from from bird banding data (Table A3; Walters 2004). We assumed female helpers have the same mortality rates as male helpers.

Table A6. Annual survival probabilities used for the Onslow Bight RCW population.

Class / sex	Probability of Annual Mortality
Fledgling / male	0.41
Fledgling / female	0.56
Helper / male	0.18
Helper / female	0.18
Breeder / male	0.17
Breeder / female	0.21
Floater / male	0.30
Floater / female	0.30

Reproduction

The number of fledglings produced by each breeding group was estimated based on the influence of demographic and climate factors on productivity (Table A7). We compiled demographic data from 628 breeding events, involving 304 breeding pairs, spanning the years 1997 to 2009, because weather data were also available during this time. The number of active territories within 800m of each territory center was also estimated. Because productivity reflects the cumulative influence of environmental conditions on the energetics of birds prior to and including the season of reproduction, we used seasonal averages prior to the mating season (Summer: July, August, September; Fall: October, November, December; and Winter: January, February, March) and the season in which mating and fledging occurs (Spring: April, May, June). These seasonal averages were derived as described in Section 2 above.

We first estimate the probability of successful breeding defined as producing at least one fledgling, using logistic regression (i.e., binomial model using a logit link function). In the second step, we estimated the factors that led to n fledglings given that the breeding pair was successful. Poisson regression using a log link function was used for this second step. Because both steps involve repeated measures of fledglings generated by a given breeding pair, mixed model regression was used in which breeding pair, a categorical variable, was treated as a random effect and demographic and climatic variables were treated as fixed effects (lmer function in R; R Development Core Team 2010).

Table A7. Two models were estimated to predict fledglings per group, a logistic and poisson regression, which predict the probability of successful breeding (LogLik = -297, AIC_c = 613) and the number of fledglings given at least one fledgling was produced (LogLik = -55.8, AIC_c = 120), respectively.

P(Fledglings>0) = logit (p(x))				
	Estimate	Std. Error	z value	P(> z)
Intercept	-12.5	3.50	-3.58	0.000346
age_m	0.744	0.150	4.97	0.000000673
age_f	0.591	0.128	4.61	0.00000401
age_m2	-0.0457	0.0107	-4.27	0.0000199
age_f2	-0.0428	0.0104	-4.11	0.0000393
Fa_aveF	0.236	0.0630	3.74	0.000182
Wi_wind	-1.49	0.434	-3.44	0.000576
Su_wind	0.567	0.234	2.42	0.0153
act800	-0.187	0.121	-1.55	0.121
Log(E(Fledglings=n Fledglings>0)) = log(λ(z))				
	Estimate	Std. Error	z value	P(> z)
Wi_avmaxF	0.0127	0.00183	6.90	0.00000000000529
help_m	0.1247	0.0382	3.26	0.00111
Wi_prec	-0.0475	0.0293	-1.62	0.105

$$P(\text{Success}) = \frac{e^{b_0 + b_1 \text{Age}_m + b_2 \text{Age}_f + b_3 \text{Age}_m^2 + b_4 \text{Age}_f^2 + b_5 \text{FallTemp} + b_6 \text{WinterWind} + b_7 \text{SummerWind} + b_8 \text{Active800}}}{1 + e^{b_0 + b_1 \text{Age}_m + b_2 \text{Age}_f + b_3 \text{Age}_m^2 + b_4 \text{Age}_f^2 + b_5 \text{FallTemp} + b_6 \text{WinterWind} + b_7 \text{SummerWind} + b_8 \text{Active800}}}$$

$$E(\text{Fledglings}) = e^{b_9 \text{WinterTemp} + b_{10} \text{Helper}_m + b_{11} \text{WinterPrec}}$$

Reproduction was modeled by drawing a u[0,1] random numbers and comparing it to the probability of success estimate for that breeding pair. If successful, the Poisson regression equation

was used to estimate the number of fledglings. The expected number of fledglings was then used as the estimate of lambda pulled at random from a Poisson distribution.

Add Immigrants

This submodel adds one new immigrant that is assumed to be unrelated to all birds included in the simulation. One such unknown immigrant is added every four years, or One Migrant Per Generation.

Nei

The expected apportionment of genetic variance within and among breeding groups was estimated by the method of Nei (1973). Total genetic diversity in the population (H_T) was apportioned into components including the average genetic diversity within breeding groups (H_S) and average genetic divergence among breeding groups (D_{ST}), $H_T = H_S + D_{ST}$. Nei defines total genetic diversity (H_T) as the probability that any two alleles chosen at random are independent. Average gene diversity within breeding groups (H_S) equals the probability that two alleles chosen at random from within an individual are independent, averaged across the breeding groups. D_{ST} represents the probability that two genes are different when chosen at random from individuals in two different breeding groups (i.e., habitat patches) averaged across the entire population. This method uses allele frequencies of the current population avoiding unrealistic assumptions regarding random uniting of gametes, rates of drift within groups, or patterns of migration among groups (Nei 1986), making it useful for describing genetic diversity in dynamic landscapes.

Under the LEA Approach, the Nei submodel also includes estimates of effective population size (N_e) directly based on the change in genetic variation over time. By using an SEPM, we directly simulate demographic and behavioral components of the actual population that deviate from the ideal Wright-Fisher population (e.g., overlapping generations, variance in reproductive success, mating system, fluctuating population size, and asymmetric immigration). N_e can be estimated to reflect the different processes that lead to the change in genetic variation (e.g., inbreeding (N_eI) and variance (N_eV) effective population size estimate the size of a genetically ideal population losing genetic variation due to inbreeding and drift, respectively).

N_eI was estimated by the rate of change in total observed heterozygosity (H_0) at the infinite alleles locus (Wright 1969; Harris & Allendorf 1989):

$$H_{Ot} = H_{Oo}(1 + 1/2N_eI)^t$$

$$N_eI = 1/(-2e^m + 2)$$

where

$$m = d \log(H_{Ot})/d t$$

where t is measured in generations. By definition, homozygous genotypes at this locus are identical by descent.

N_eV was estimated based on the change in allele frequency p in the diallelic locus of the fledglings (Whitlock & Barton 1997):

$$V_t = p_t(1 - p_t)F_t$$

$$\Delta V = (V_{t+1} - V_t)/(p_o q_o - V_t)$$

$$N_e V = 1/2\Delta \bar{V}$$

where

$$F_t = 1 - H_{ot}$$

$$q_o = 1 - p_o$$

Competition

Competition was simulated largely as described in Letcher et al. (1998). However, a recent radiotelemetry study (Kelser et al. 2010) revealed competition behaviors different than assumptions included in Letcher et al. (1998). It was previously assumed that foray distance, defined as the distance at which a bird can detect and compete for a breeding vacancy, was three km. The recent radiotelemetry results suggest six km as an upper bound on foray distance. We incorporated uncertainty regarding a bird's foray distance by allowing this value to vary from one to 60 cells, or six km, for helpers and floaters of both sexes. Results from this study also suggested that the presence of non-forested gaps between a bird's current location and a breeding vacancy may prevent a bird from detecting and competing for that breeding vacancy. We updated the model to included parameters to turn gap avoidance behaviors on or off during competition for breeding vacancies. We included parameters to turn gap avoidance on or off for water and terrestrial gaps during competition for males and females. It was possible for a parameterization to simulate gap avoidance during competition for only terrestrial gaps or both water and terrestrial gaps. If a gap greater than 150 m was present between a competitor's current location and the breeding vacancy and gap avoidance behaviors were turned on, the individual was unable to compete for the vacancy. However, if gap avoidance was turned off, individuals could compete for any breeding vacancy within its perceptual distance regardless of gaps.

Male-Male Competition

First, we assume that all helpers will preferentially inherit their natal territory upon the death of the breeding male (Walters et al., 1988). If more than one helper is present in a territory when the male breeder dies, we assume the oldest helper wins the territory (Walters et al., 1988). When a helper inherits his natal territory, the female breeder becomes a floater to avoid incest. If the male breeder dies and no helpers are present, it has been observed that 83% of the time the female breeder remains in the territory and acquires a new mate (Daniels and Walters, 2000). It is assumed that widowed females remain in territories until a new male can be established (Letcher et al., 1998). Next competition for widowed female breeders occurs. The model assumes that helpers, male floaters, and solitary male breeders within 3.5 km of the widowed female will compete. The closest male wins the breeding vacancy, if equidistant the oldest male wins (Letcher et al., 1998). Third, competition for vacant territories occurs within 3.5 km of all helpers and male floaters in the area, applying the same rules stated above.

Female-Female Competition

We assume that females only compete for territories containing solitary males and do not defend territories as solitary females (Walters et al., 1988). The pool of female competitors includes all displaced female breeders due to inbreeding avoidance and floaters within 3.5 km of the solitary male. The oldest female wins the vacancy, following Letcher et al. (1998). If there is more than one female of that maximum age, the winner is selected at random. If a female had been a breeder in that territory at a previous time or was born in that territory, she is not allowed to win the territory.

Natal dispersal

The probability of a male and female fledgling delaying dispersal and staying as a helper was estimated directly from CL's bird banding database for the years 1997-2009. For males the probability of dispersal was 0.112 and for females it was 0.629. Following Letcher et al. (1998), each fledgling had a 0.33 probability of dispersing in Summer, Fall, or Winter.

Translocate (LEA Approach only)

Translocation is a user selected submodel, which if not selected will result in natural colonization of mitigation territories (see Add Mitigation Territories above). To simulate the managed movement of birds from CL to mitigation territories, we first identified all sets of "connected components". A connected component is a set of 6 mitigation territories that can be made available for RCWs by the current year of the simulation and are within 3.2 km of a recruitment cluster with another nearest neighbor within 3.2 km which may or may not be already occupied by RCWs. Each connected component is given a score to reflect the number of occupied territories within 3.2 km. The territories in the connected component with the highest score are then made available for RCWs. This connected component receives 3 male and 3 female floaters that were selected randomly from CL. Birds from CL are selected from those fledglings that remained in Fall. Male fledglings were selected from CL territories with at least one male helper present. No more than two female fledglings could be selected from any territory on CL. Once these fledglings are translocated as floaters they compete for breeding vacancies in the six territories within the connected component using the competition rules described below. Importantly, if floaters are in the area due to simulated dispersal processes (i.e., and not translocation), these translocated birds would then have to compete with floaters for the vacancies. To simulate the lower success of translocated birds (McDearman 2011), seasonal probability of survival for translocated birds that become breeders was adjusted from 0.95 to 0.63.

Dispersal

Results from the recent radiotelemetry work in the Sandhills Region of NC (Kesler et al. 2010) suggested that birds tend to cross gaps less than 150 m but rarely crossed gaps greater than 600 m, changing their direction of travel to stay within forested areas. A dispersal kernel we refer to as a Gap/Jump dispersal model was derived to capture this dynamic. We estimate the probability of a female crossing gaps > 150 m and < 600 m by:

$$P = 1 + \beta G$$

Where, β is a fitted coefficient and G is gap length in meters.

It was assumed that 10% of the time birds would disperse straight through gaps greater than 600 m, in what might be referred to as jumping behavior (Kesler et al. 2010).

POM was used to estimate β for the Onslow Bight landscape within the RCW IB-SEPM. Further, POM allowed us to test new hypotheses, specifically if water gaps affect dispersal behaviors, which is more germane in the Onslow Bight landscape than in the Sandhills. This was accomplished by allowing β to vary independently, from 0 to -0.005, for water and terrestrial gaps for both males and females. We also allowed the number of dispersal steps taken per season to vary, from 1 to 20 cells, or 2 km. If the bird encounters a gap, the dispersal model sums the size of water and terrestrial gaps. For each gap > 150 m and < 600 m the above equation was used to estimate the probability of crossing the gap. If the gap is greater than 600 m then there was a 10% probability the bird would jump the gap. When each bird encounters a gap the model draws a $u[0,1]$ random number and compares it to the probability of crossing the gap. If the random number is sufficiently small the bird will not cross the gap and turns 45 deg, either right or left chosen at random, to look for a new path. If the bird turns a full 360 deg without being able to move, the bird is left in its current location until the next season at which point it still may be able to compete for a breeding vacancy, may be able to move in the next season, or will die.

Table A8. The model parameters that were indirectly estimated by POM for males and females and their initial ranges

Parameter	Range
perceptual distance of helpers	1 to 60
perceptual distance of floaters	1 to 60
seasonal dispersal distance	1 to 20
strength of terrestrial gap avoidance	0 to -0.005
strength of water gap avoidance	0 to -0.005
sensitivity to terrestrial gaps during competition	0 or 1
sensitivity to water gaps during competition	0 or 1

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APPENDIX B: PROPERTY-SPECIFIC RESULTS FOR LANDSCAPE EQUIVALENCY ANALYSIS AND PATCH-BASED SUMMARIES

Table B1. Landscape Service Years (LSYs) for each ecological service, dispersal parameterization, and scenario.

	Bear Garden		Shaken Creek		Oak Island	Oak Island & S GSRA
	Natural	Translocation	Natural	Translocation	Natural	Natural
Potential Breeding Groups (PBG)						
POM 1	4.96*	5.60*	2.58*	2.71*	2.54*	6.33*
POM 2	5.25*	5.63*	3.08*	2.89*	2.92*	6.41*
POM 3	4.77*	5.46*	2.54*	2.63*	2.31*	6.18*
POM 4	4.51*	5.13*	2.27*	2.39*	2.19*	5.88*
POM 5	5.29*	5.67*	2.73*	2.63*	2.78*	6.16*
DSS	2.00*	4.29*	2.07*	3.18*	2.35*	5.05*
Average Expected Heterozygosity within breeding groups (H_S)						
POM 1	-0.131	-0.0730	-0.0562	-0.105†	-0.0469	-0.0954
POM 2	-0.192†	-0.0830	-0.172	-0.0781	-0.172	-0.221
POM 3	-0.131‡	-0.0269	-0.0134	-0.0586	-0.0245	0.00787†
POM 4	-0.113	-0.0591	0.0448	-0.0497	-0.0116	-0.0599
POM 5	-0.00331	0.105	-0.0140	0.0641	0.0649	0.0755
DSS	-0.217	-0.102	-0.236	-0.346†	-0.131	-0.244
Average Genetic Divergence among breeding groups (D_{ST})						
POM 1	-0.436†	-0.272	-0.203	-0.343†	-0.190	-0.332
POM 2	-0.612*	-0.319†	-0.560‡	-0.327	-0.519	-0.628†
POM 3	-0.484*	-0.222‡	-0.176	-0.259‡	-0.159*	-0.135
POM 4	-0.383	-0.284	-0.00916	-0.211	-0.129	-0.235
POM 5	-0.163‡	0.0935	-0.142	0.0157	0.0447	0.0378
DSS	-0.614*	-0.333	-0.696†	-0.956‡	-0.421	-0.717†
Total Expected Heterozygosity within the population (H_T)						
POM 1	0.0195*	0.0179	0.0134‡	0.0134‡	0.0176‡	0.0172‡
POM 2	0.0191	0.0247	0.0215	0.0283	0.0167	0.00630
POM 3	0.0294*	0.0356*	0.0385*	0.0224*	0.0233*	0.0383*
POM 4	0.0209‡	0.0318‡	0.0337‡	0.0215‡	0.0260‡	0.0237‡
POM 5	0.0422*	0.0504*	0.0272‡	0.0386‡	0.0357‡	0.0452‡
DSS	0.00343†	0.0177†	0.0127†	0.00340†	0.0183†	0.0117†

* $p < 0.0001$, ‡ $p < 0.01$, † $p < 0.05$

Table B2. Median expected values at year 100 from Mitigation landscapes.

	Bear Garden		Shaken Creek		Oak Island	Oak Island & S GSRA
	Natural	Translocation	Natural	Translocation	Natural	Natural
Wright's Inbreeding Coefficient - F						
POM1	0.083	0.082	0.079	0.083	0.080	0.080
POM2	0.093	0.091	0.092	0.090	0.092	0.091
POM3	0.079	0.077	0.075	0.077	0.079	0.074
POM4	0.087	0.084	0.082	0.084	0.086	0.084
POM5	0.085	0.082	0.085	0.082	0.085	0.080
DSS	0.111	0.105	0.107	0.109	0.105	0.107
F_{ST}						
POM1	0.299	0.298	0.298	0.299	0.297	0.298
POM2	0.306	0.304	0.305	0.303	0.303	0.304
POM3	0.299	0.296	0.295	0.296	0.297	0.293
POM4	0.302	0.300	0.299	0.300	0.300	0.300
POM5	0.301	0.299	0.300	0.298	0.299	0.298
DSS	0.321	0.316	0.317	0.318	0.316	0.316
Potential Breeding Groups						
POM1	414	415	379	380	385	407
POM2	414	414	379	380	385	408
POM3	415	413	379	379	385	407
POM4	415	416	379	380	386	409
POM5	419	418	383	383	389	411
DSS	370	394	359	363	368	390

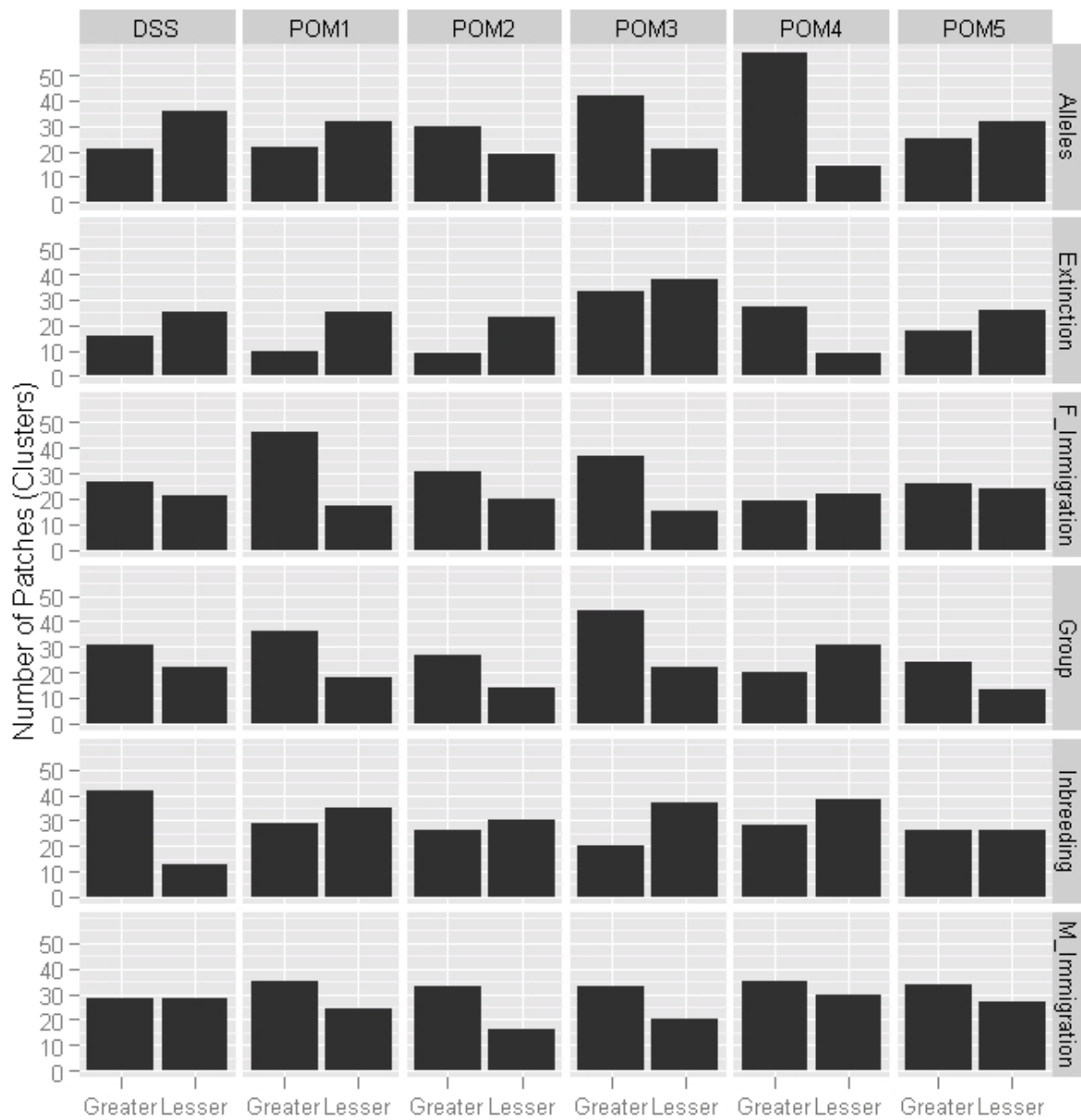


Figure B1. Number of patches found across CL, HS, and CNF with p-values ≤ 0.1 for random permutation testing of mean difference in attribute values for landscapes with and without Bear Garden, assuming natural colonization. Difference in mean attribute value may be greater or lesser than zero due to addition of Bear Garden, so p-values for both cases are presented.

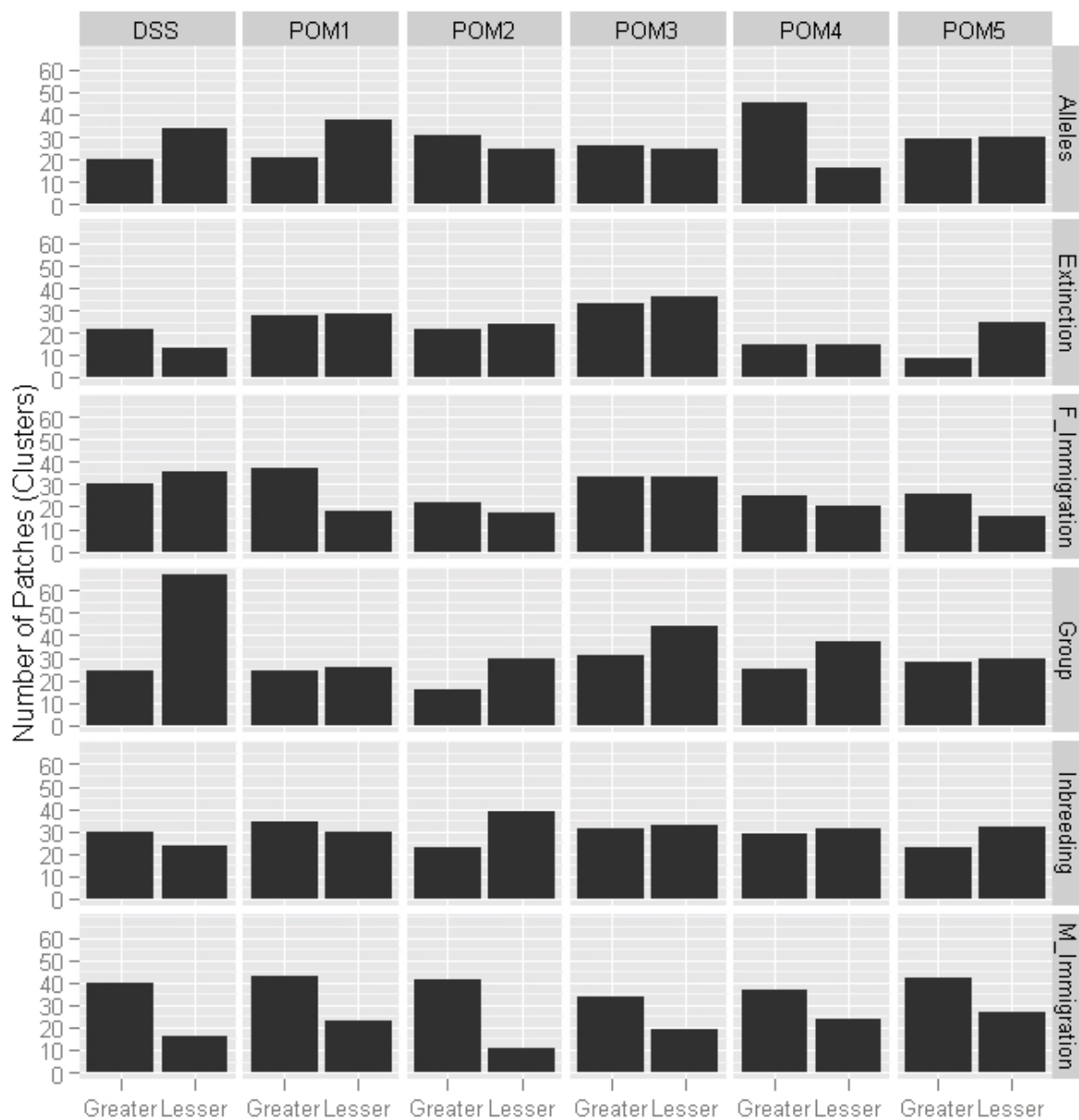


Figure B2. Number of patches found across CL, HS, and CNF with p-values ≤ 0.1 for random permutation testing of mean difference in patch values for landscapes with and without Bear Garden, assuming translocation. Difference in mean patch value may be greater or lesser than zero due to addition of Bear Garden, so p-values for both cases are presented.

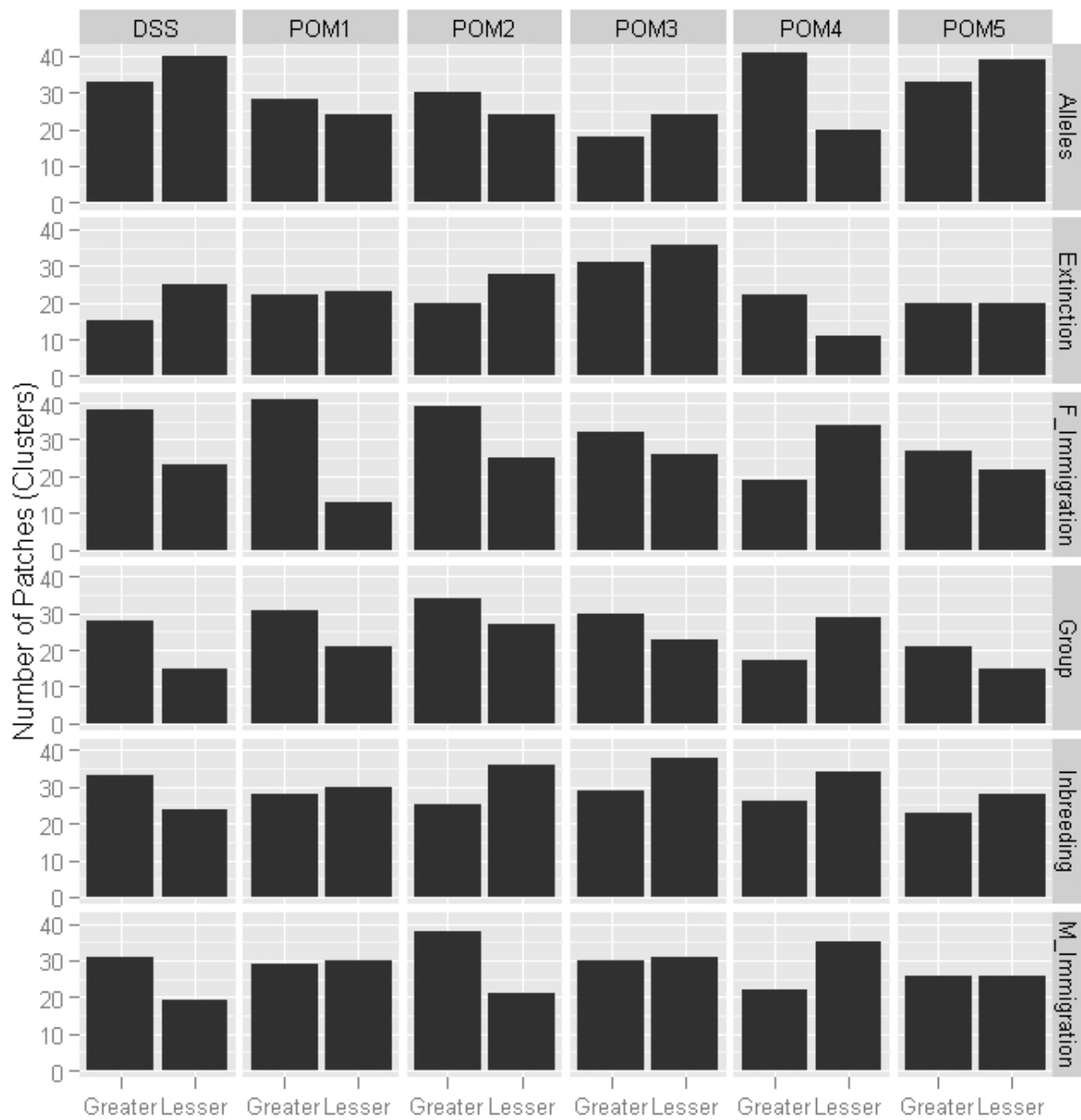


Figure B3. Number of patches found across CL, HS, and CNF with p-values ≤ 0.1 for random permutation testing of mean difference in attribute values for landscapes with and without Shaken Creek, assuming natural colonization. Difference in mean attribute value may be greater or lesser than zero due to addition of Shaken Creek, so p-values for both cases are presented.

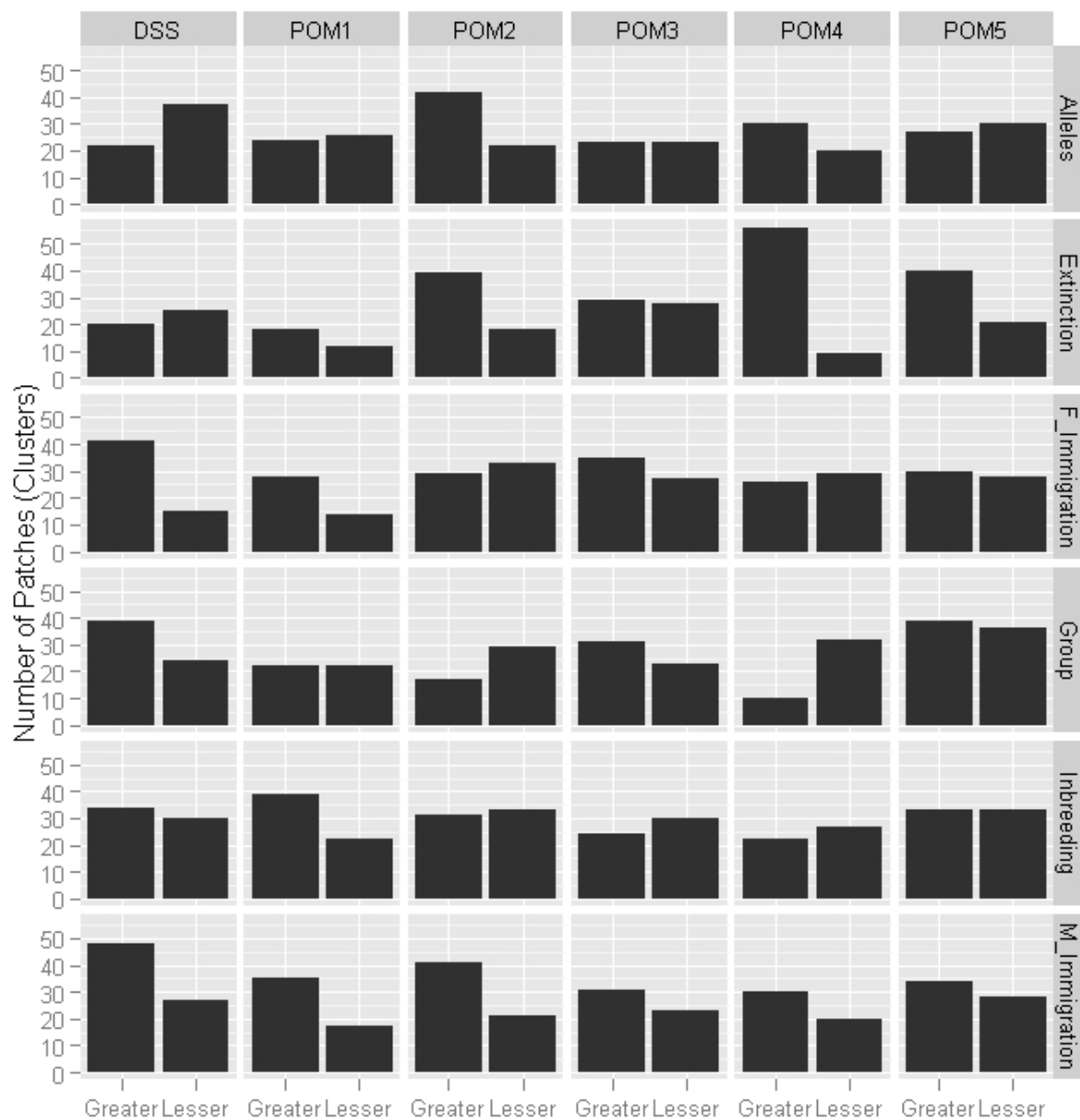


Figure B4. Number of patches found across CL, HS, and CNF with p-values ≤ 0.1 for random permutation testing of mean difference in patch values for landscapes with and without Shaken Creek, assuming translocation.

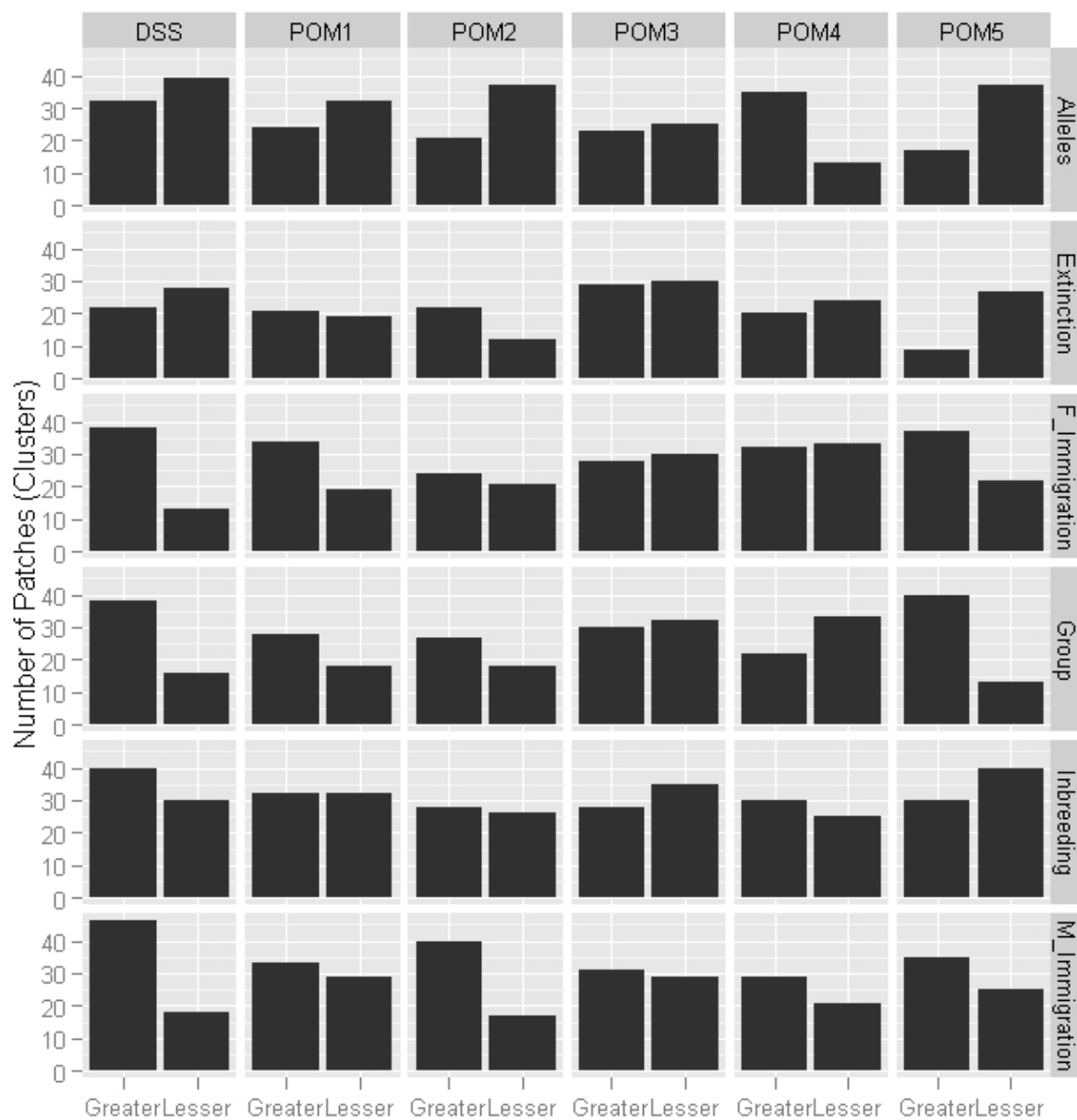


Figure B5. Number of patches found across CL, HS, and CNF with p-values ≤ 0.1 for random permutation testing of mean difference in patch values for landscapes with and without Oak Island, assuming natural colonization. Difference in mean patch value may be greater or lesser than zero due to addition of Oak Island, so p-values for both cases are presented.

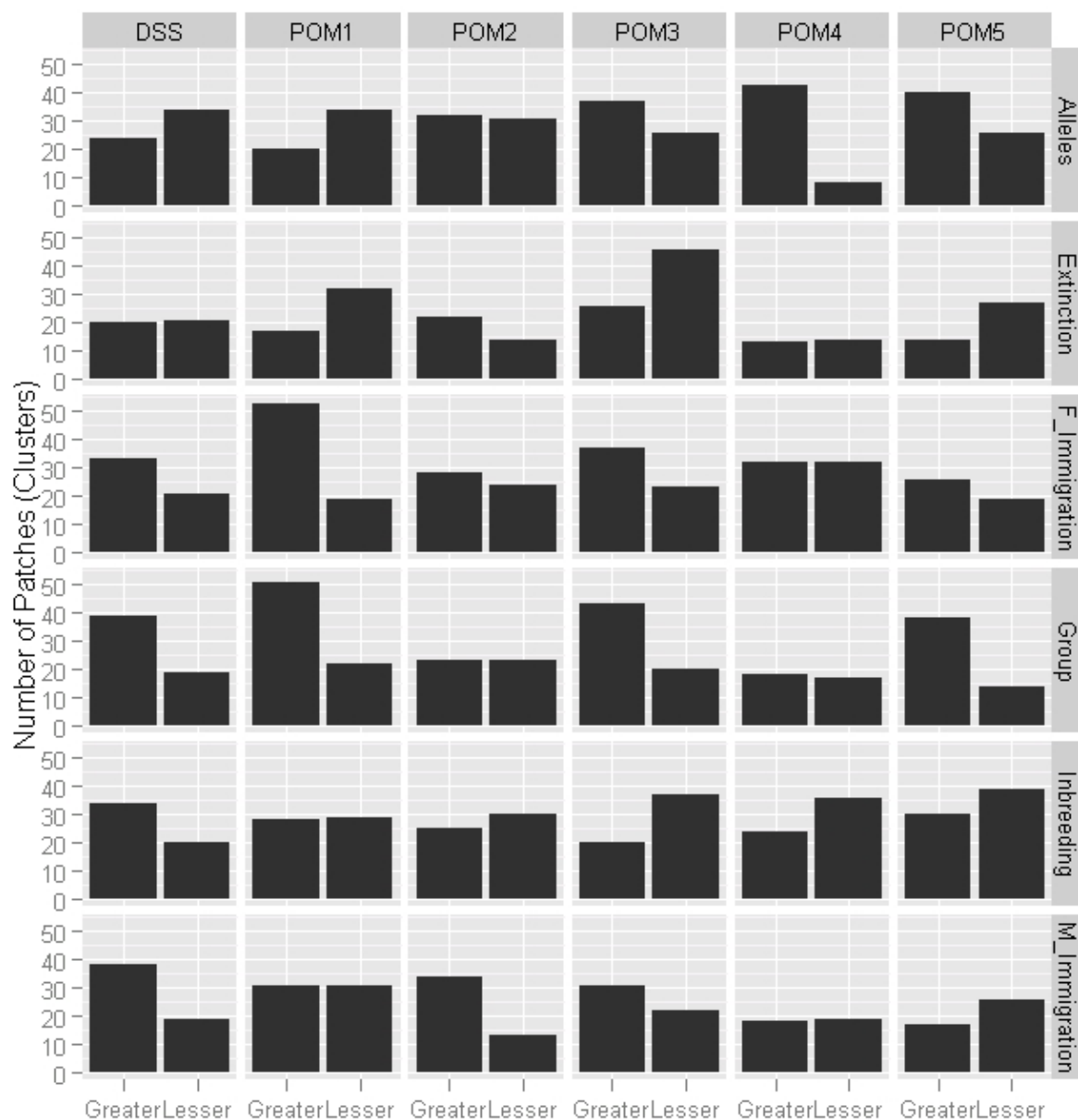


Figure B6. Number of patches found across CL, HS, and CNF with p-values ≤ 0.1 for random permutation testing of mean difference in patch values for landscapes with and without Oak Island and sGSRA, assuming natural colonization. Difference in mean patch value may be greater or lesser than zero due to addition of Oak Island and sGSRA, so p-values for both cases are presented.

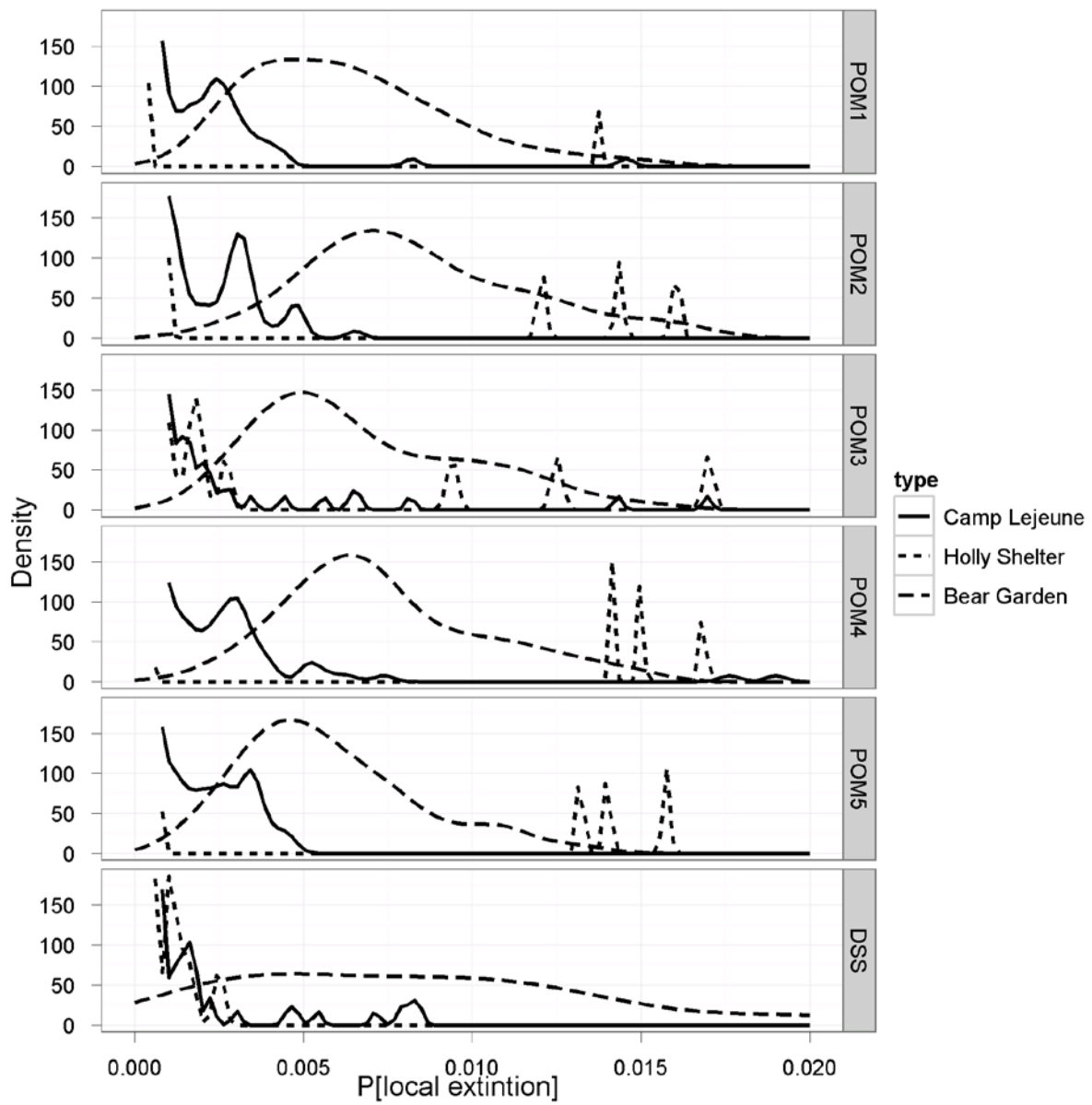


Figure B7. Distribution of patch-(territory-)based attributes summarized by property for probability of local extinction averaged over the number of years the patch was available for occupancy.

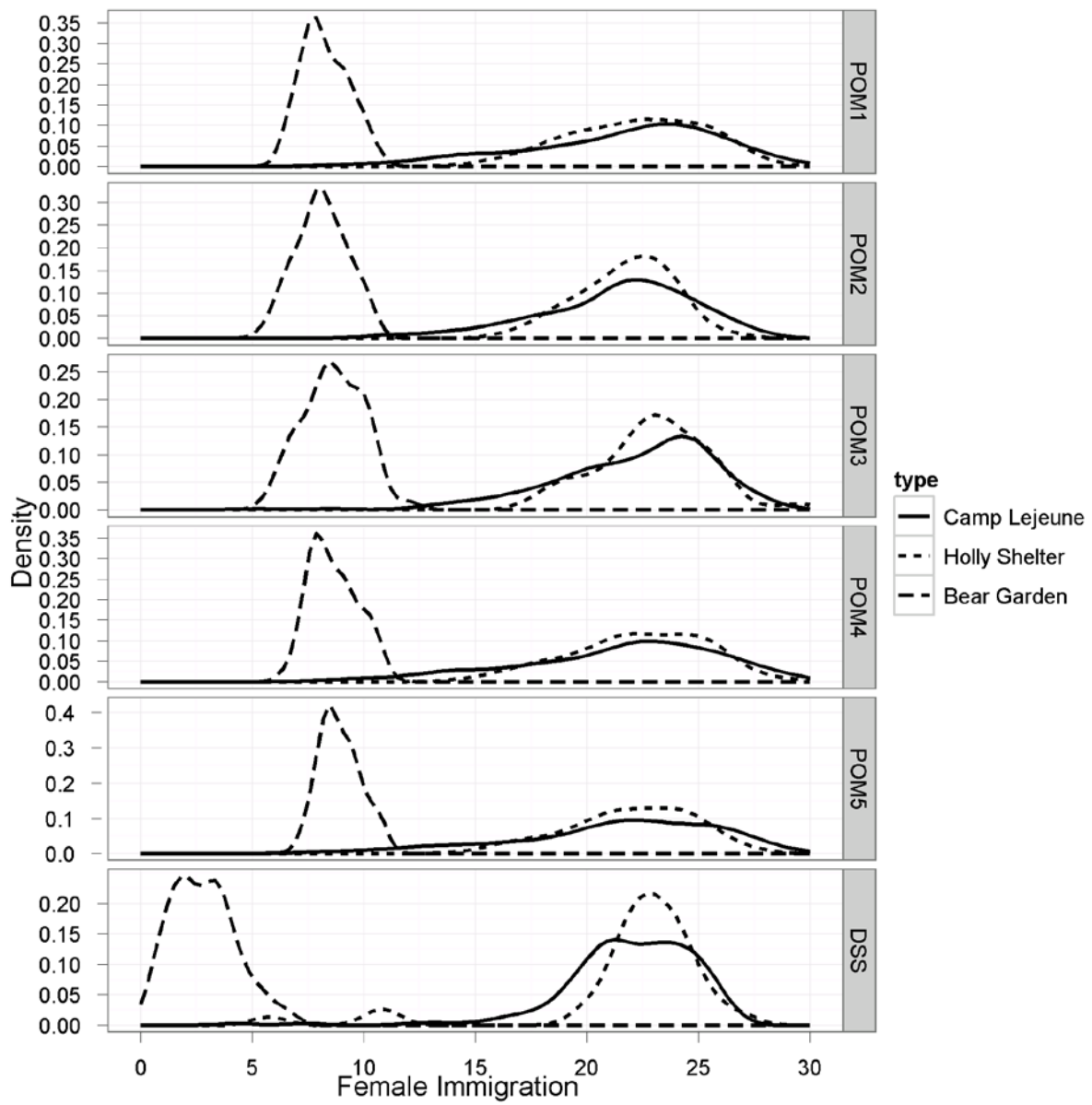


Figure B8. Distribution of patch-(territory-)based attributes summarized by property for total number of female migrants received by a patch.

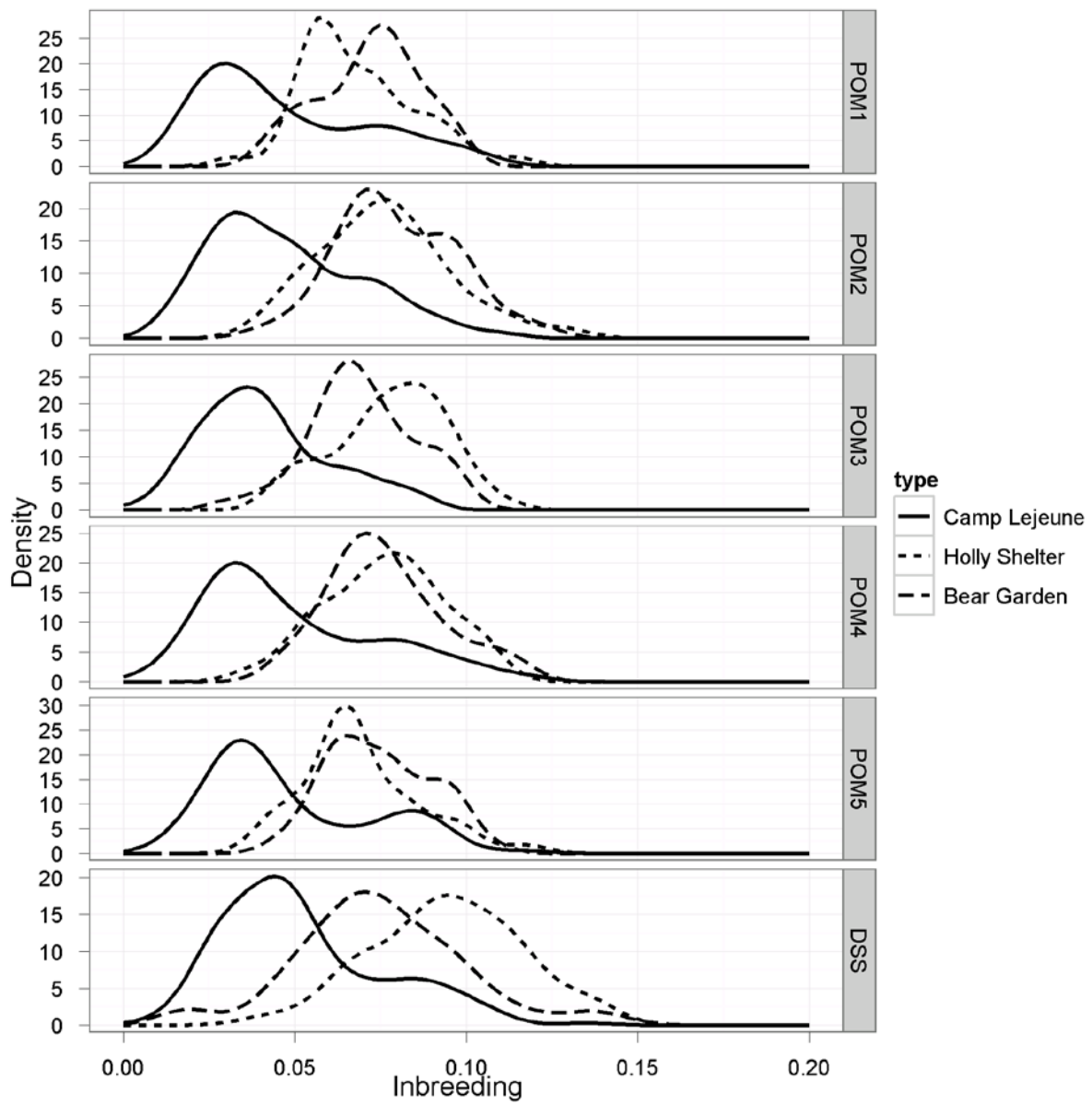


Figure B9. Distribution of patch-(territory-)based attributes summarized by property for Wright's Inbreeding coefficient at year 100.

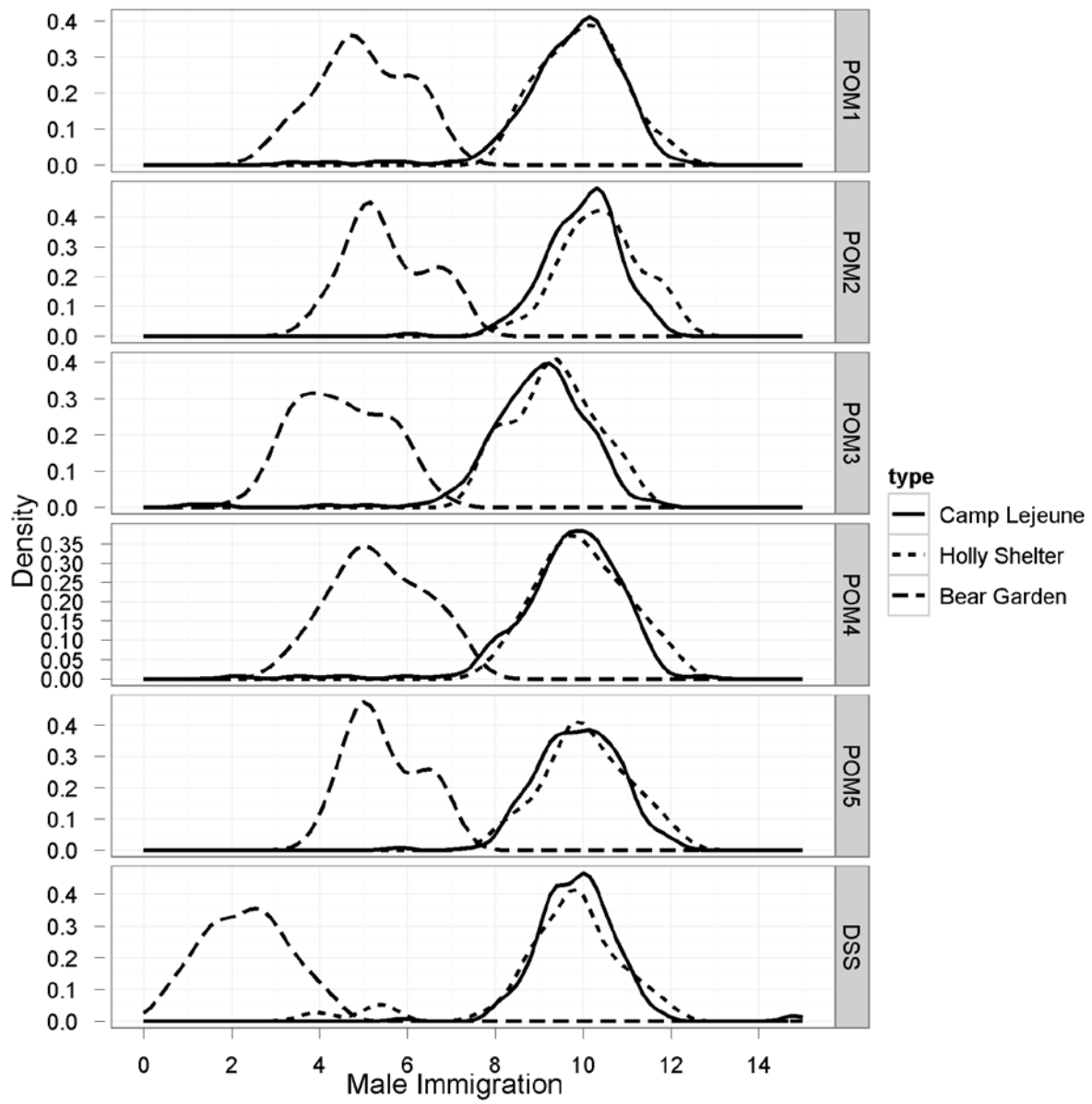


Figure B10. Distribution of patch-(territory-)based attributes summarized by property for total number of male migrants received by a patch.

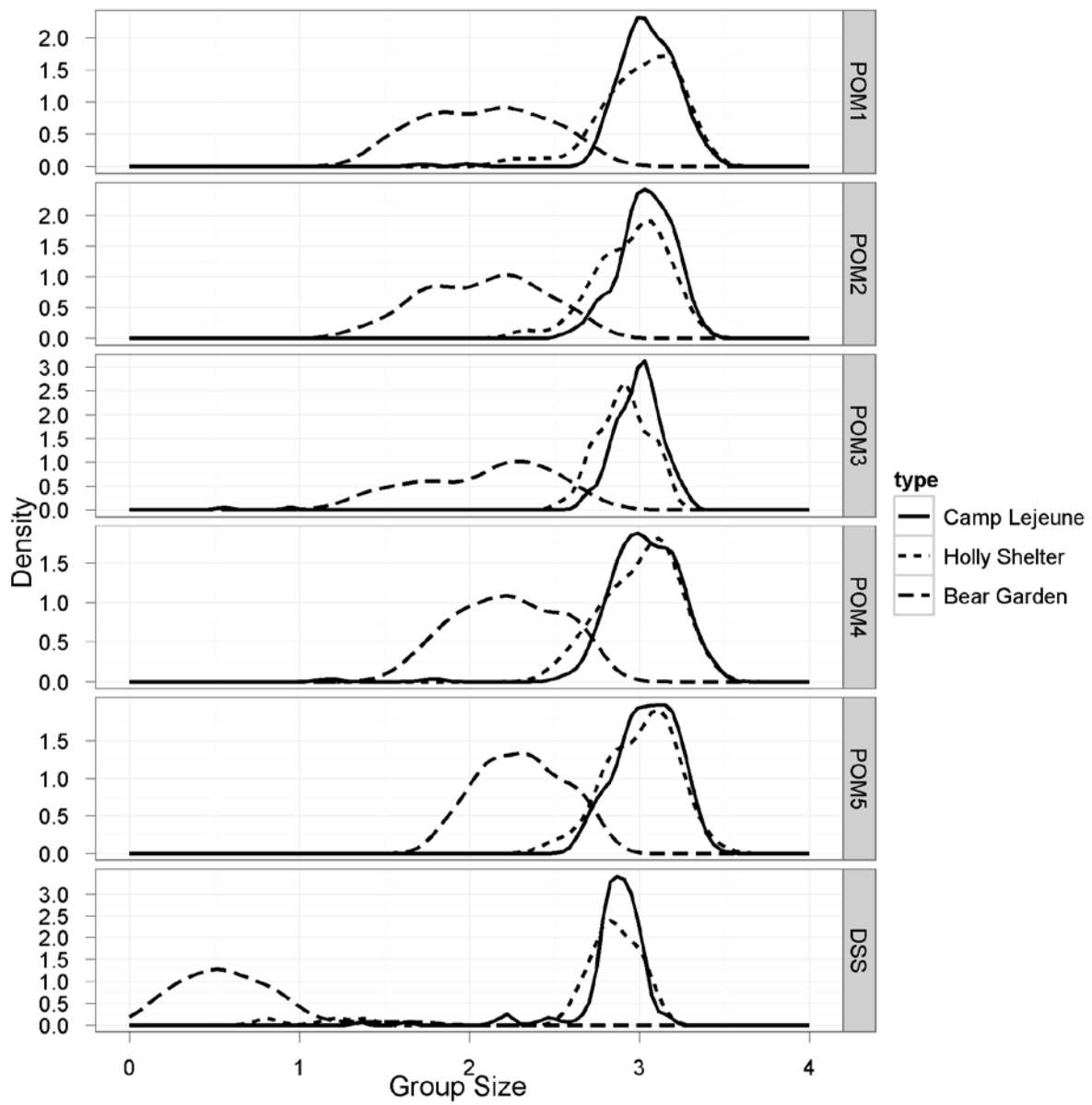


Figure B11. Distribution of patch-(territory-)based attributes summarized by property for group size (number of breeders and helpers) averaged over the number of years the patch was available for occupancy

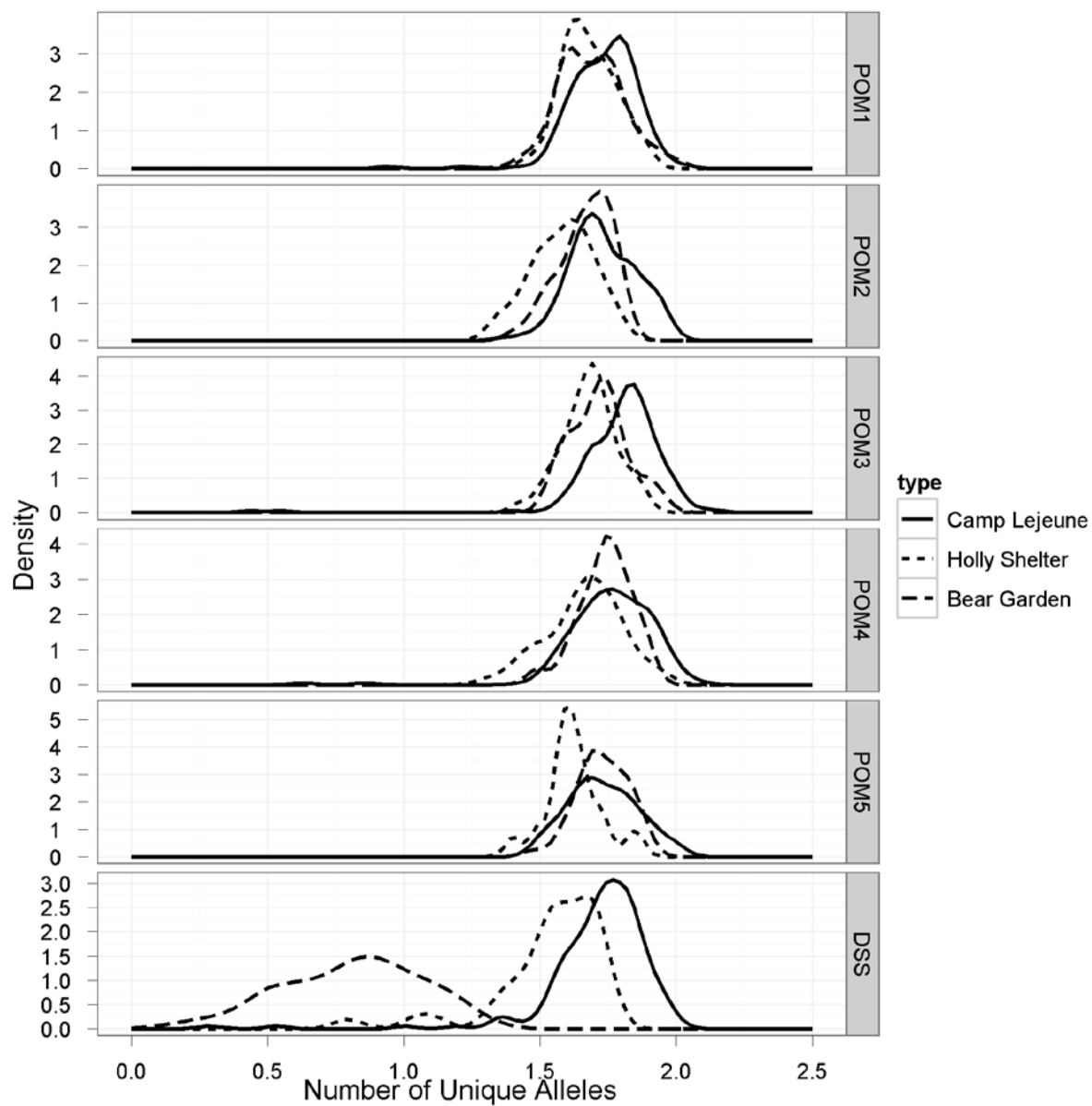


Figure B12. Distribution of patch-(territory-)based attributes summarized by property for number

Appendix B

of unique alleles at locus 2 ($sd = 1.0$) at year 100.

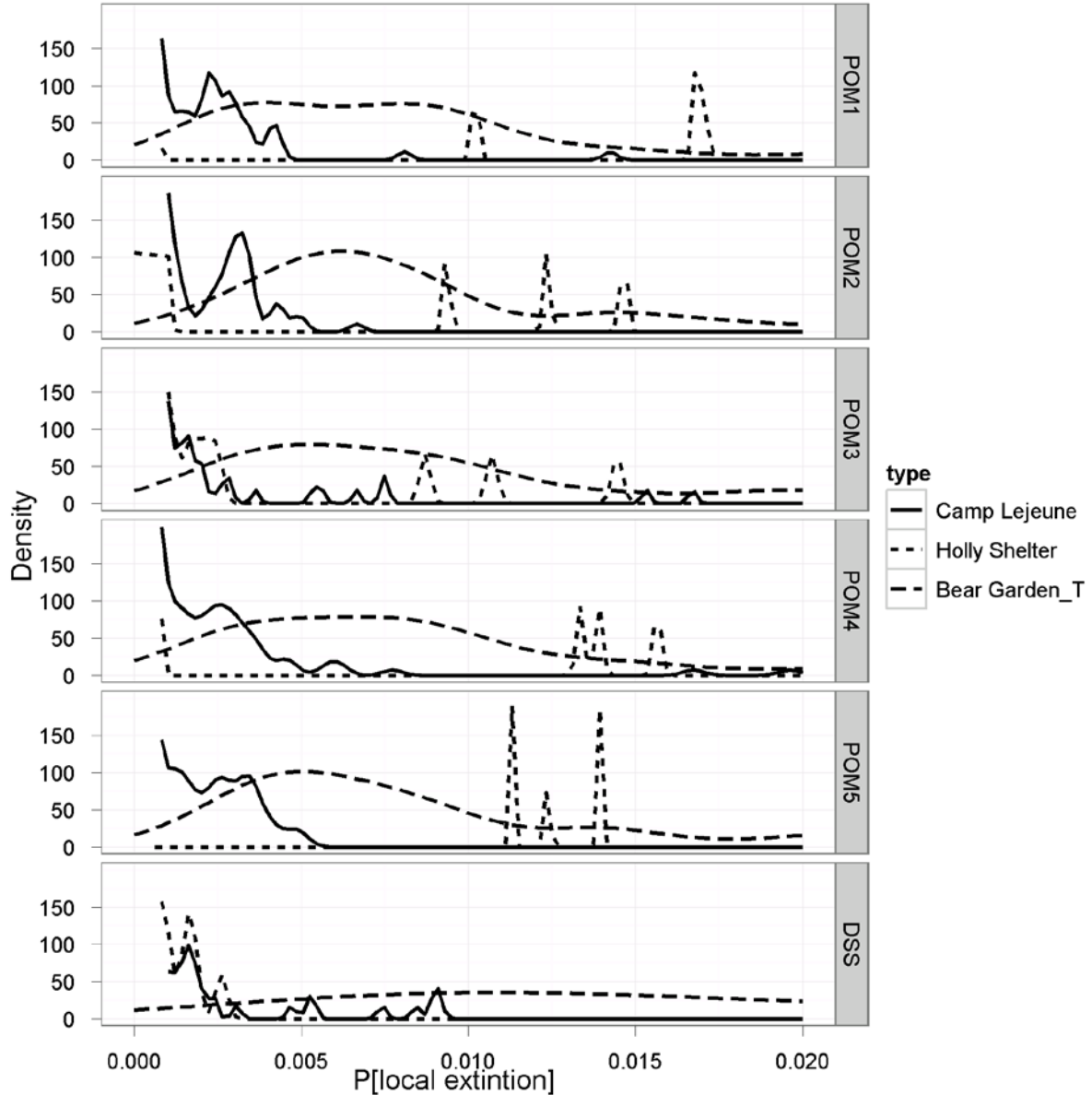


Figure B13. Distribution of patch-(territory-)based attributes summarized by property for probability of local extinction averaged over the number of years the patch was available for occupancy.

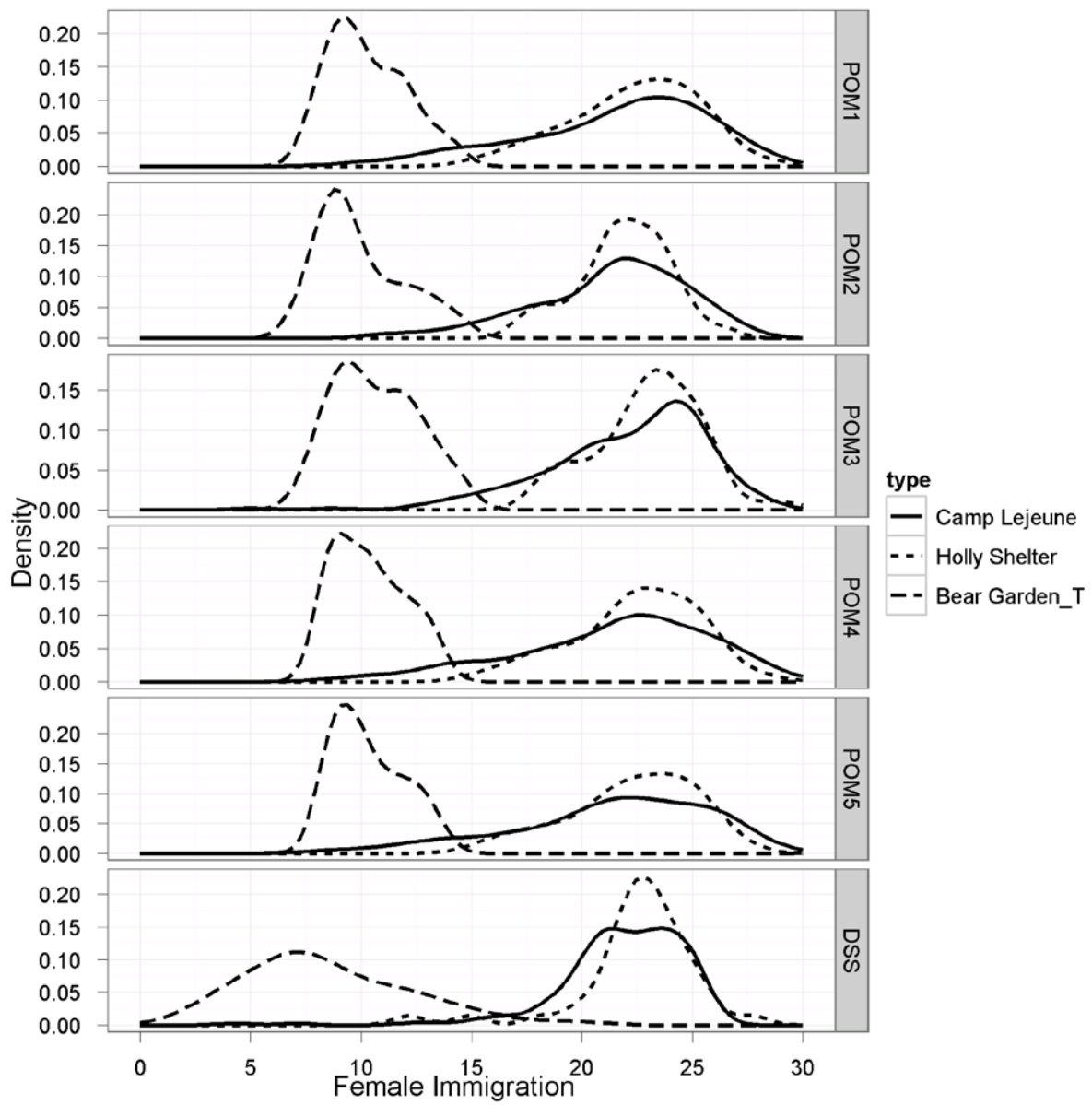


Figure B14. Distribution of patch-(territory-)based attributes summarized by property for total number of female migrants received by a patch.

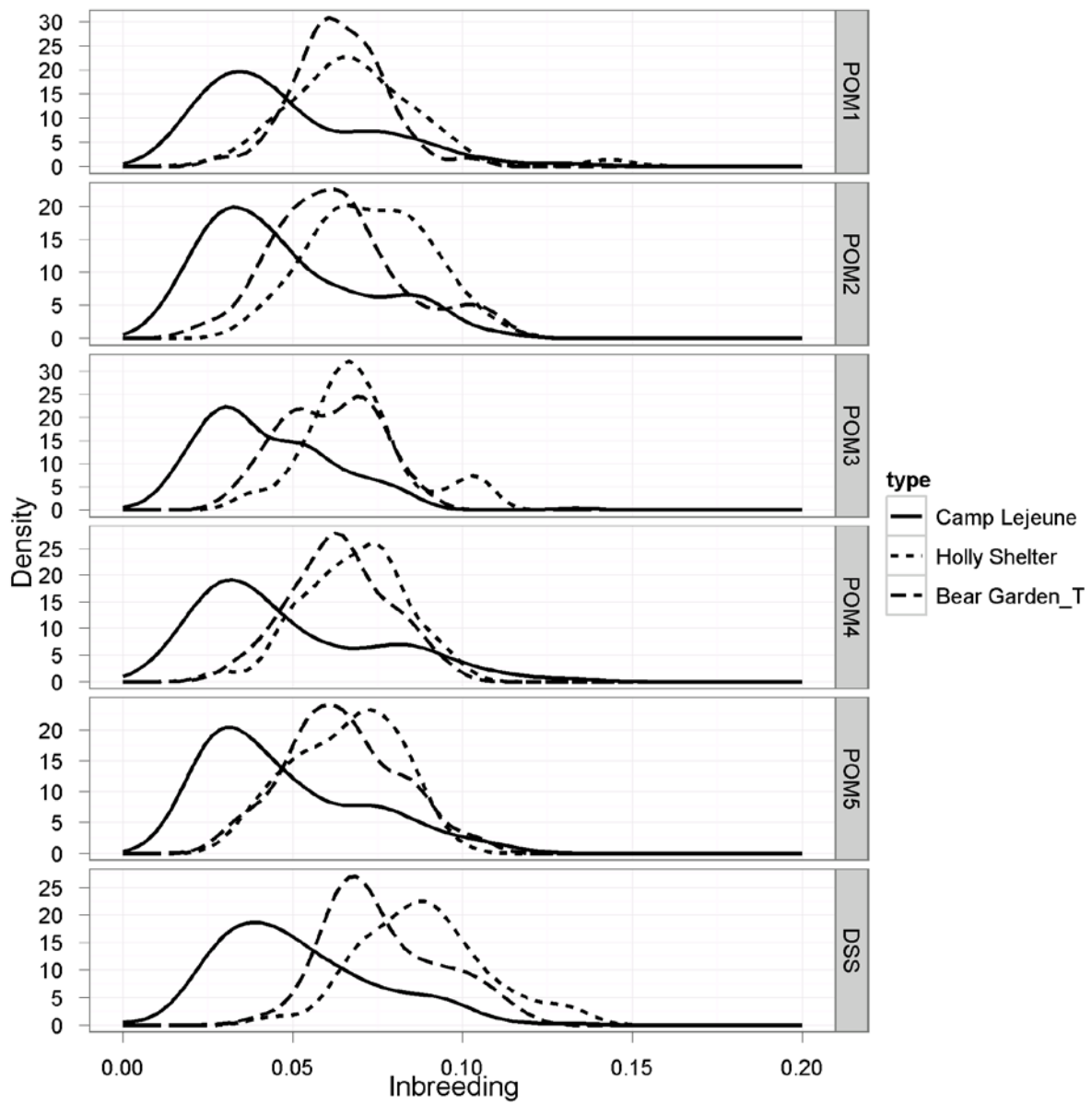


Figure B15. Distribution of patch-(territory-)based attributes summarized by property for Wright's Inbreeding coefficient at year 100.

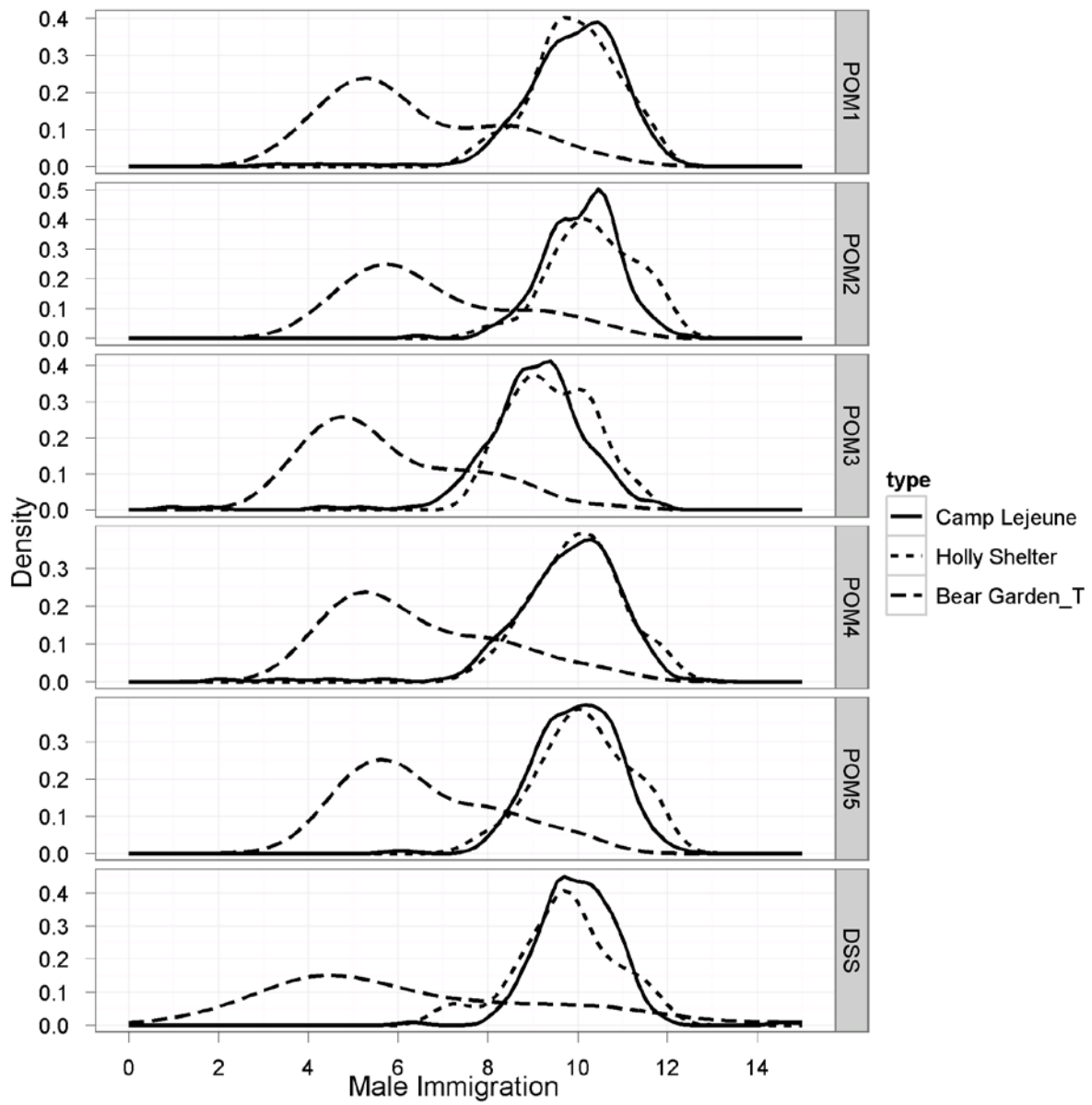


Figure B16. Distribution of patch-(territory-)based attributes summarized by property for total number of male migrants received by a patch.

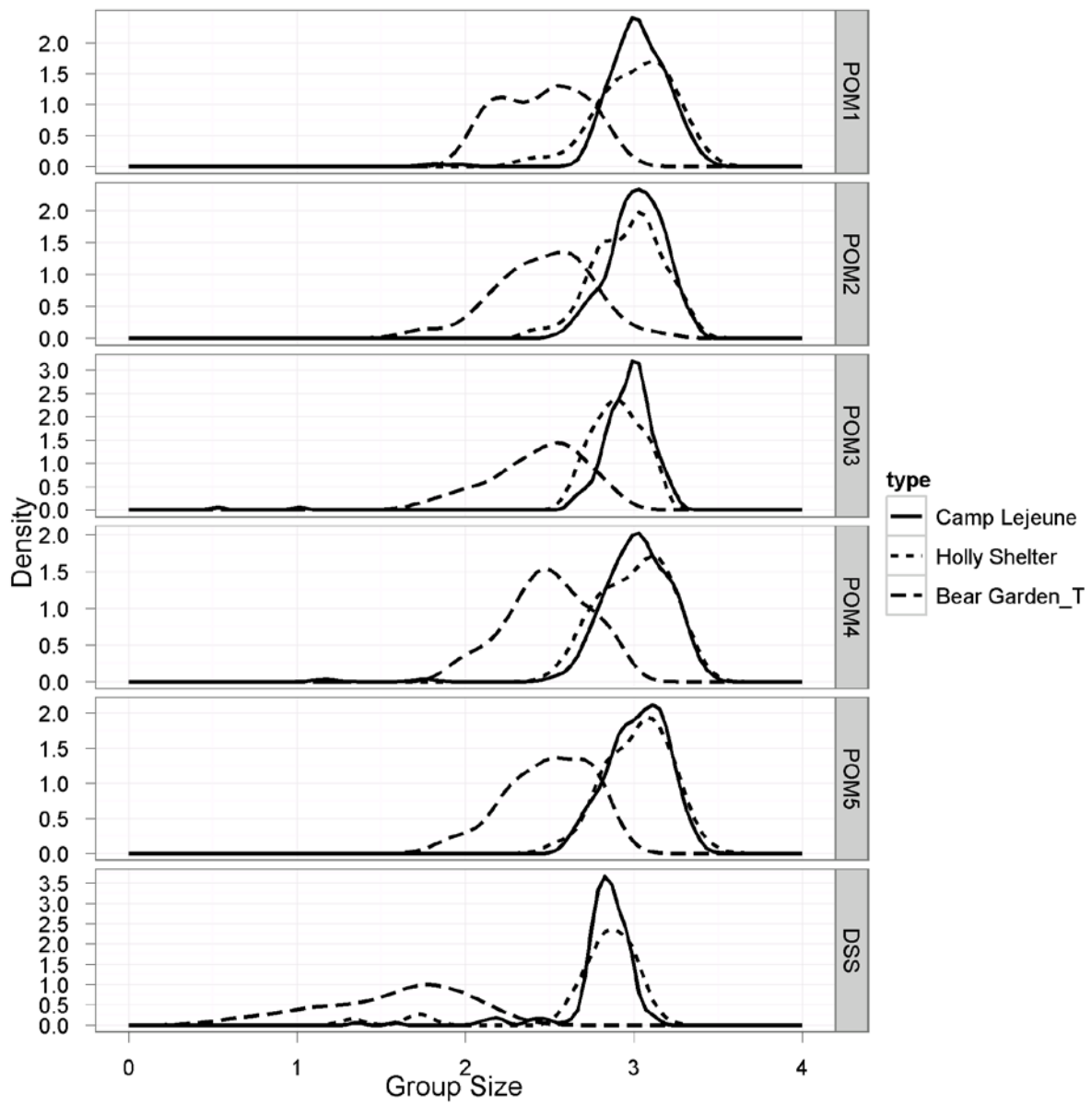


Figure B17. Distribution of patch-(territory-)based attributes summarized by property for group size (number of breeders and helpers) averaged over the number of years the patch was available for occupancy

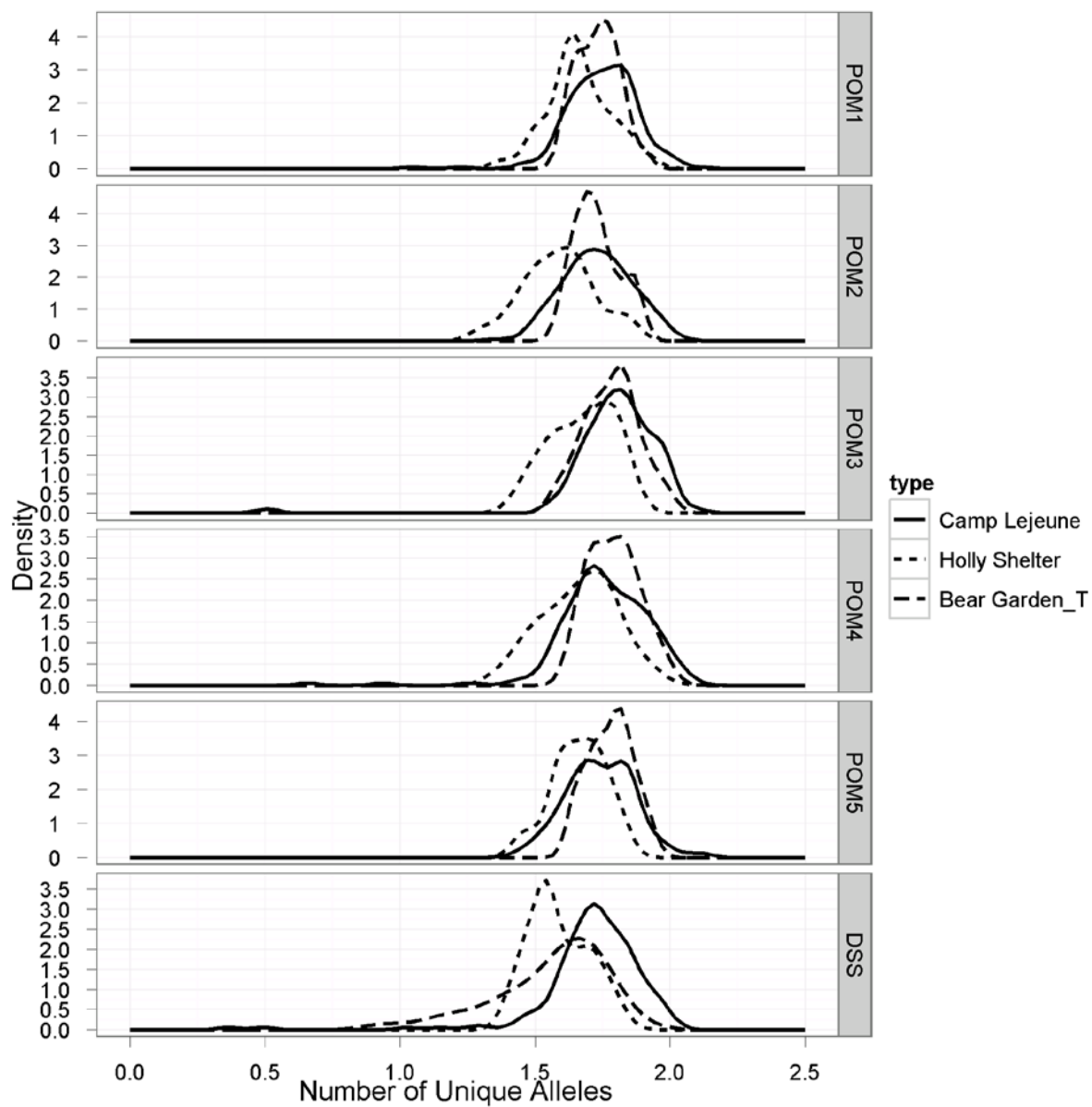


Figure B18. Distribution of patch-(territory-)based attributes summarized by property for number of unique alleles at locus 2 ($sd = 1.0$) at year 100.

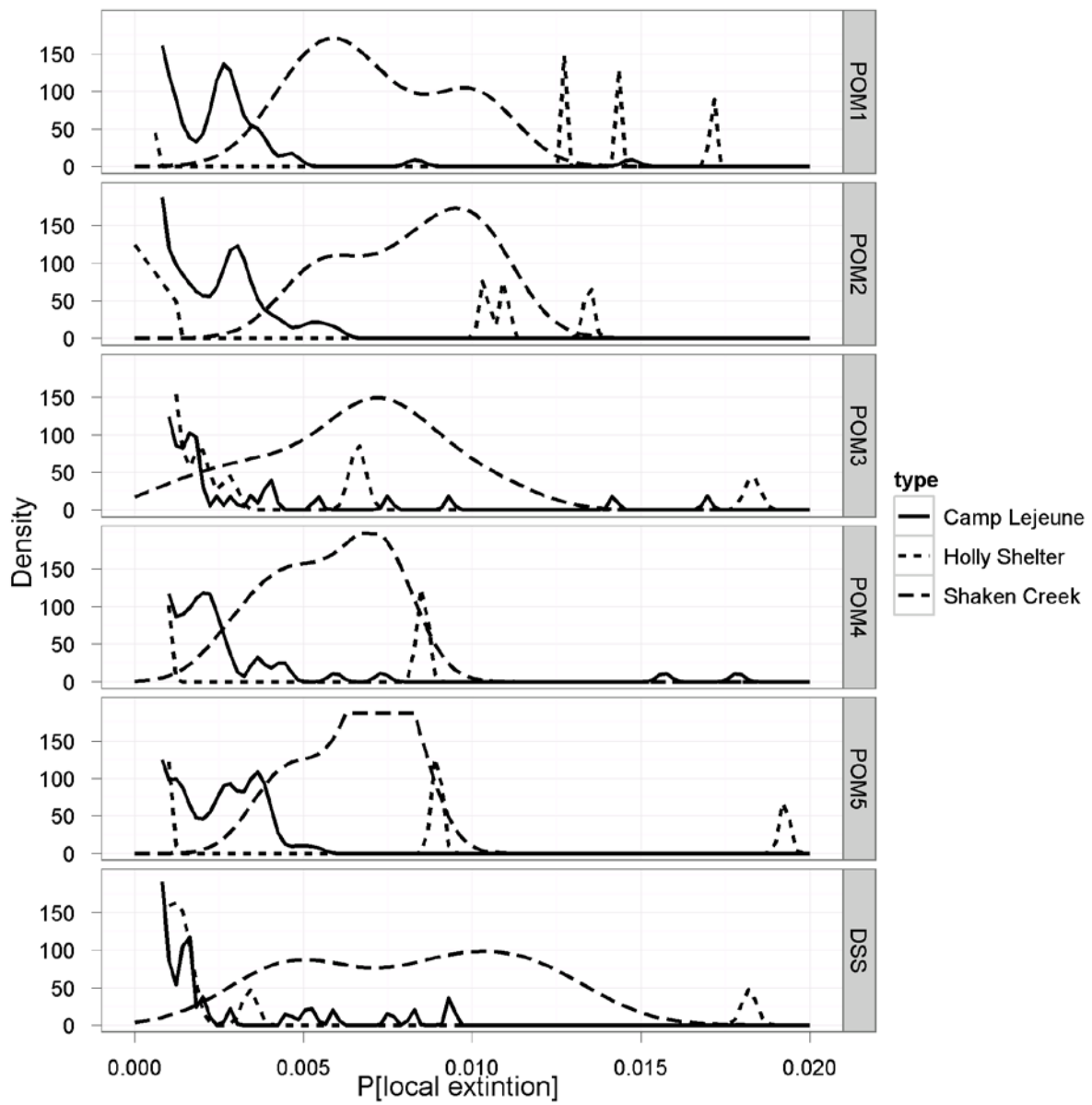


Figure B19. Distribution of patch-(territory-)based attributes summarized by property for probability of local extinction averaged over the number of years the patch was available for occupancy.

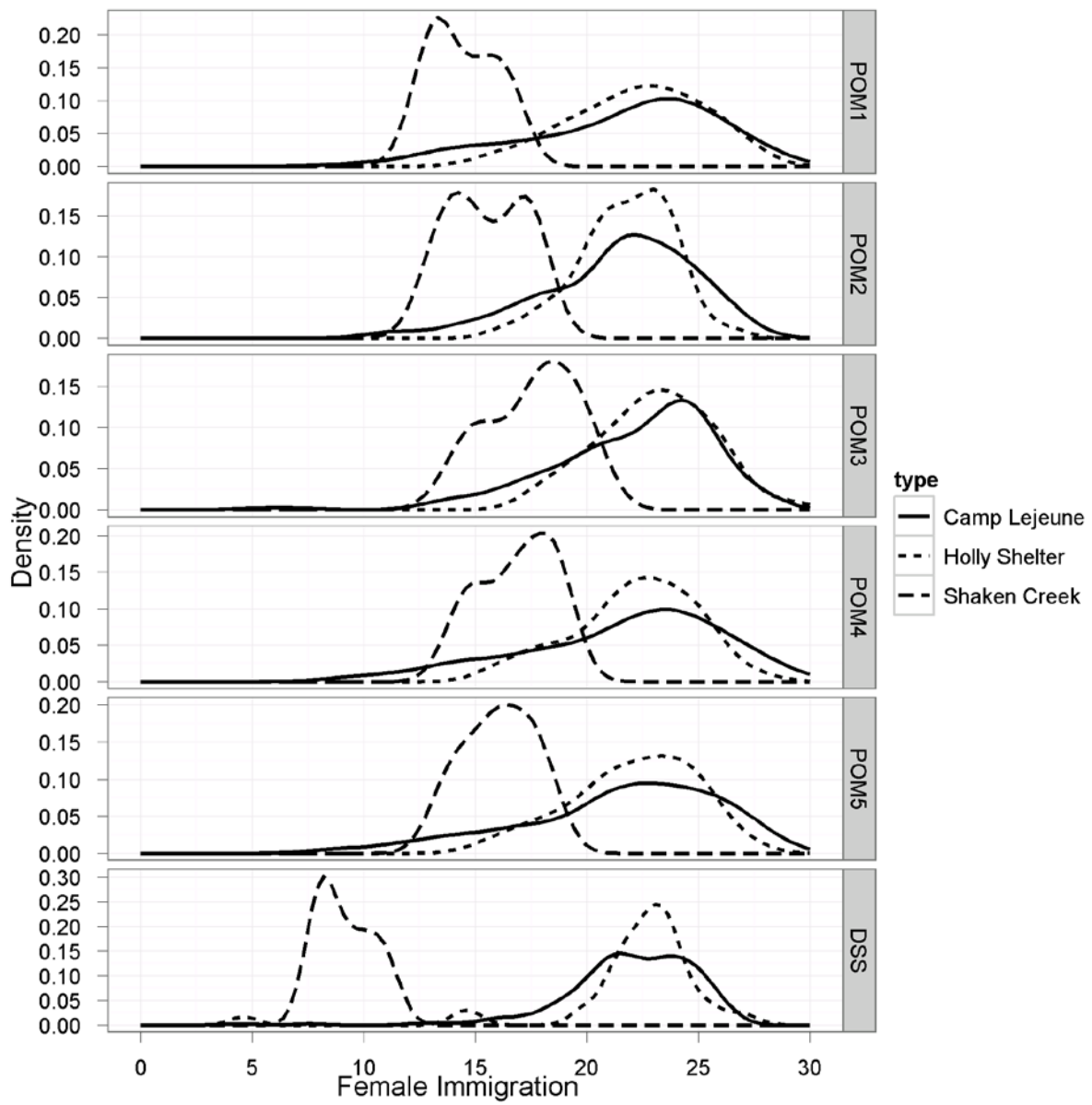


Figure B20. Distribution of patch-(territory-)based attributes summarized by property for total number of female migrants received by a patch.

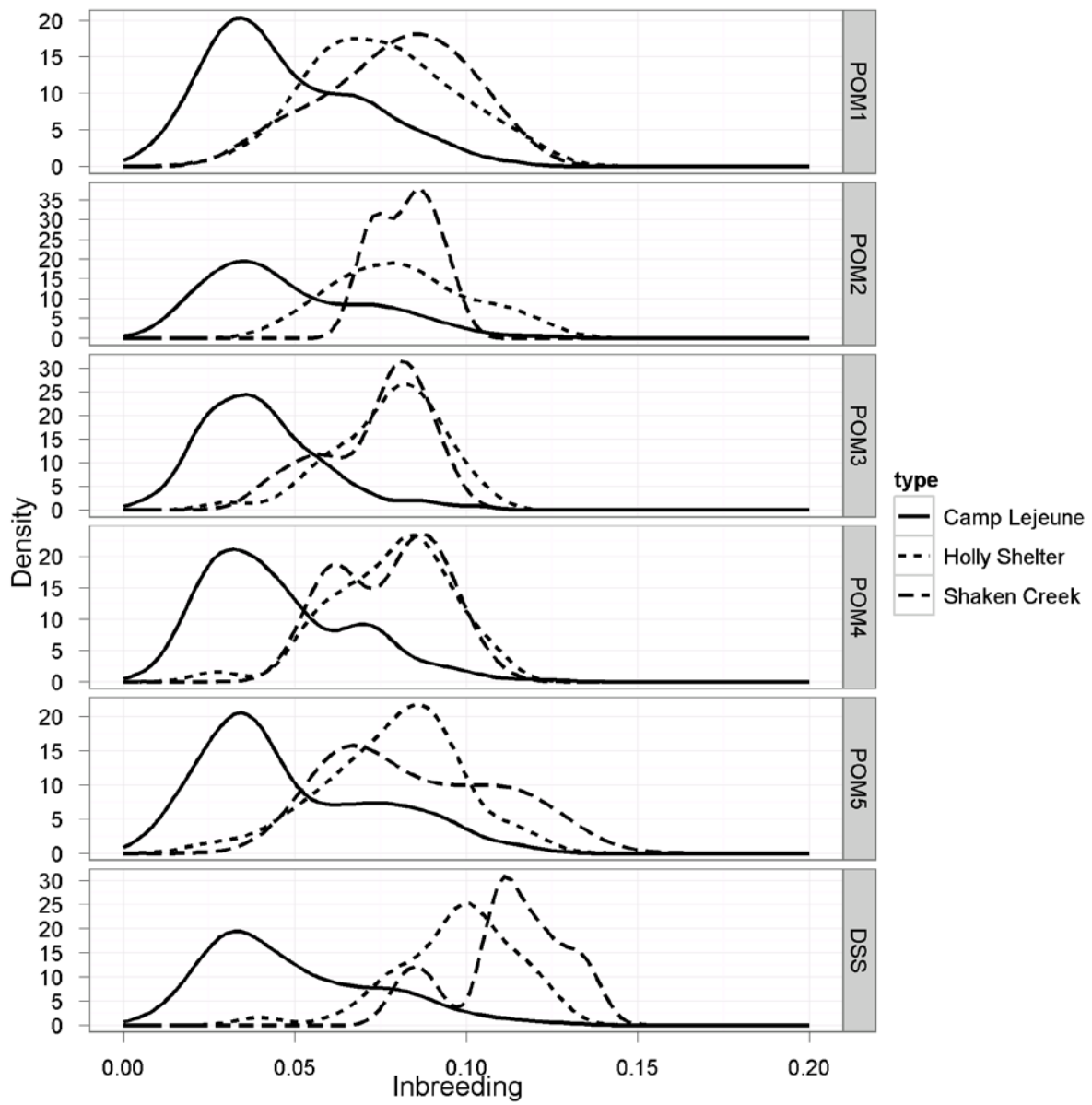


Figure B21. Distribution of patch-(territory-)based attributes summarized by property for Wright's Inbreeding coefficient at year 100.

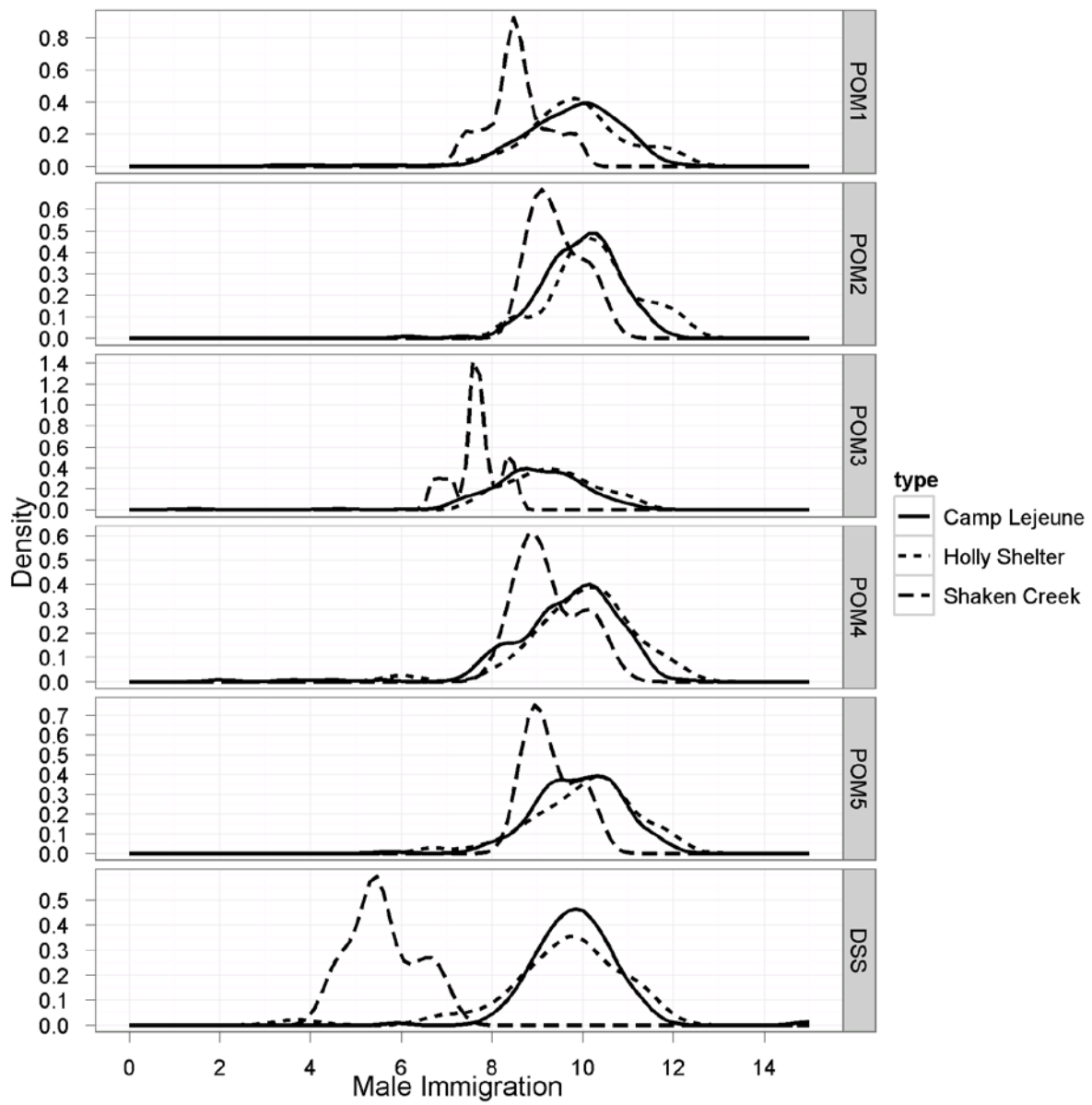


Figure B22. Distribution of patch-(territory-)based attributes summarized by property for total number of male migrants received by a patch.

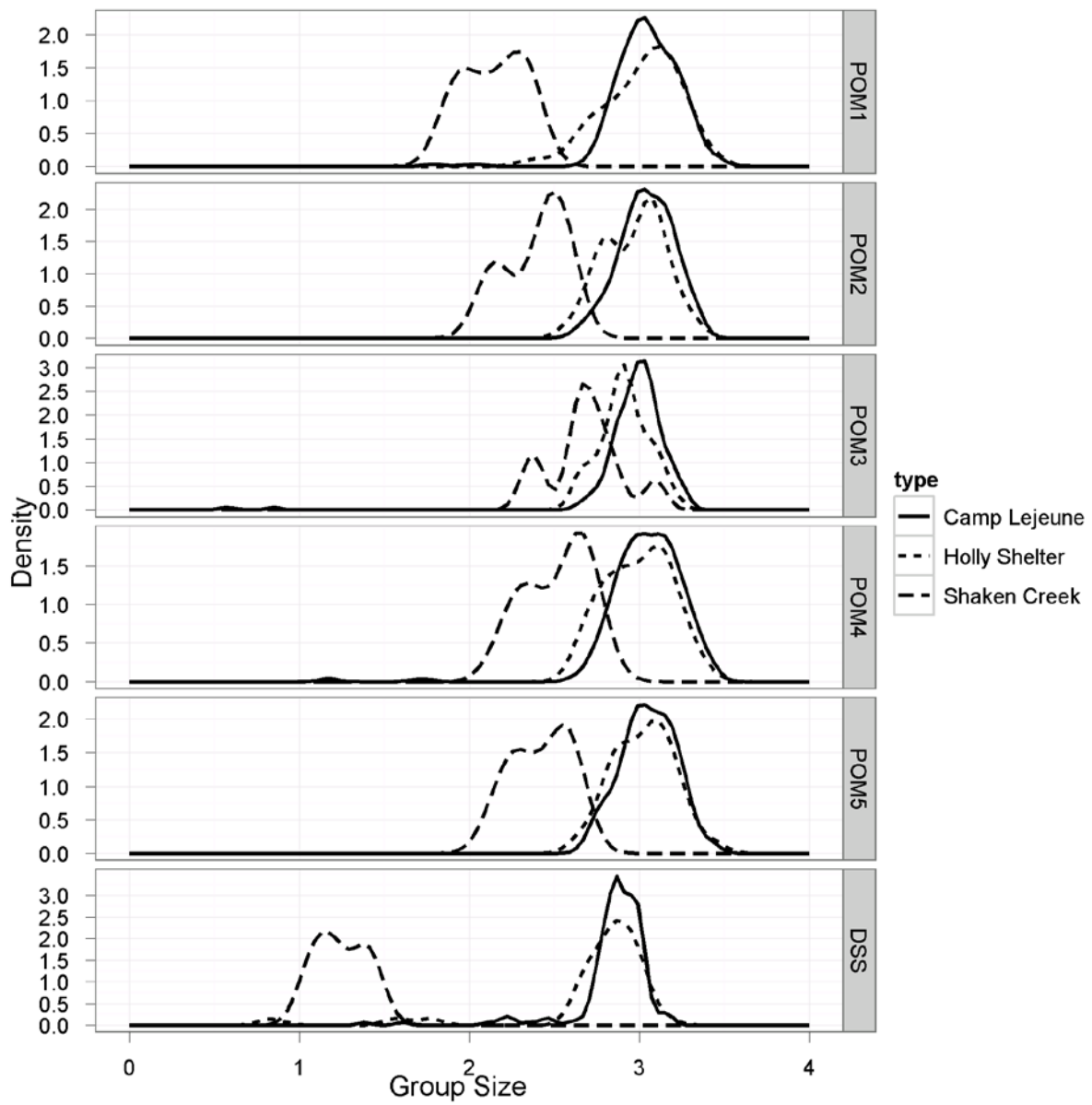


Figure B23. Distribution of patch-(territory-)based attributes summarized by property for group size (number of breeders and helpers) averaged over the number of years the patch was available for occupancy

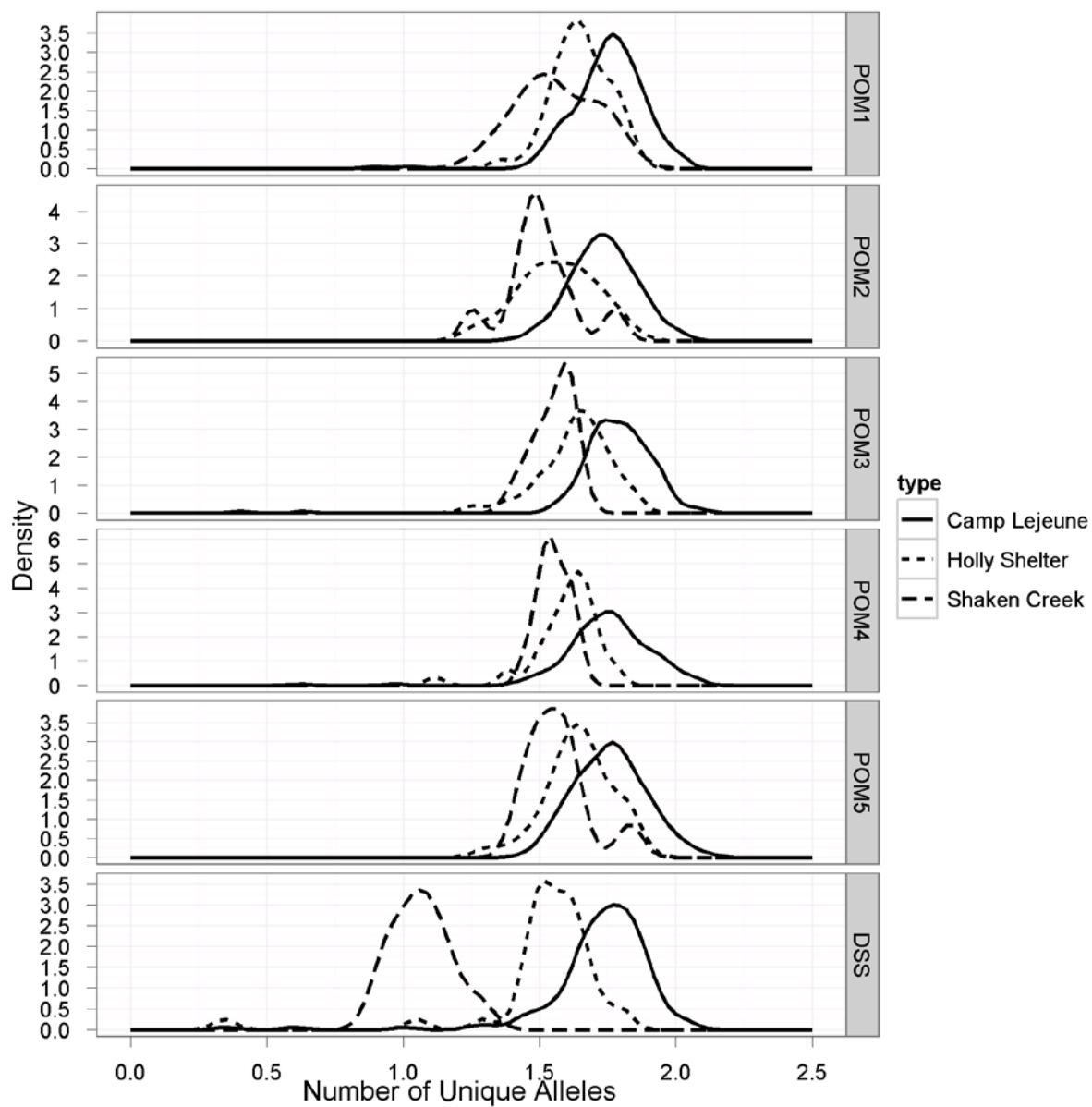


Figure B24. Distribution of patch-(territory-)based attributes summarized by property for number of unique alleles at locus 2 ($sd = 1.0$) at year 100.

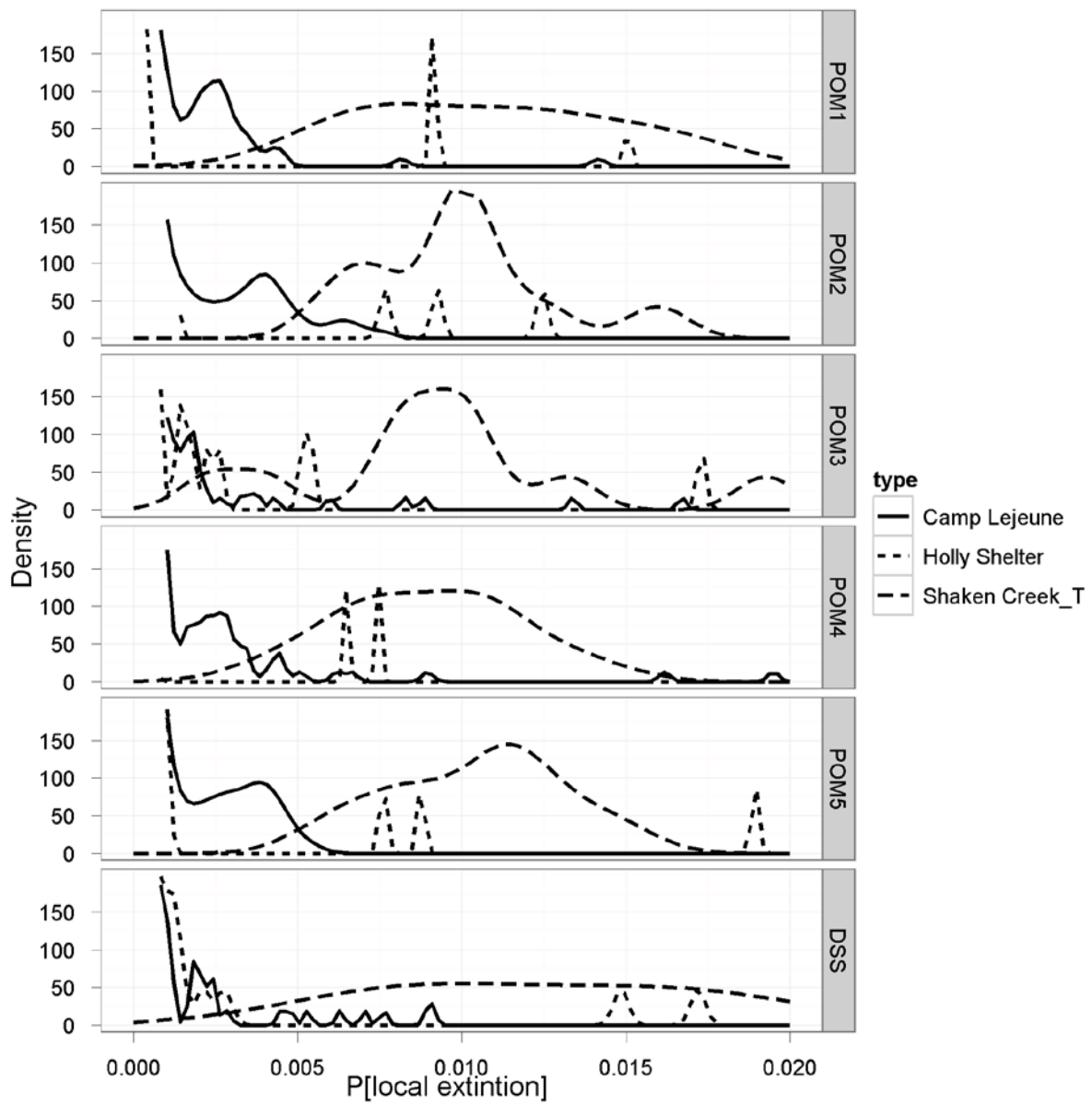


Figure B25. Distribution of patch-(territory)-based attributes summarized by property for probability of local extinction averaged over the number of years the patch was available for occupancy.

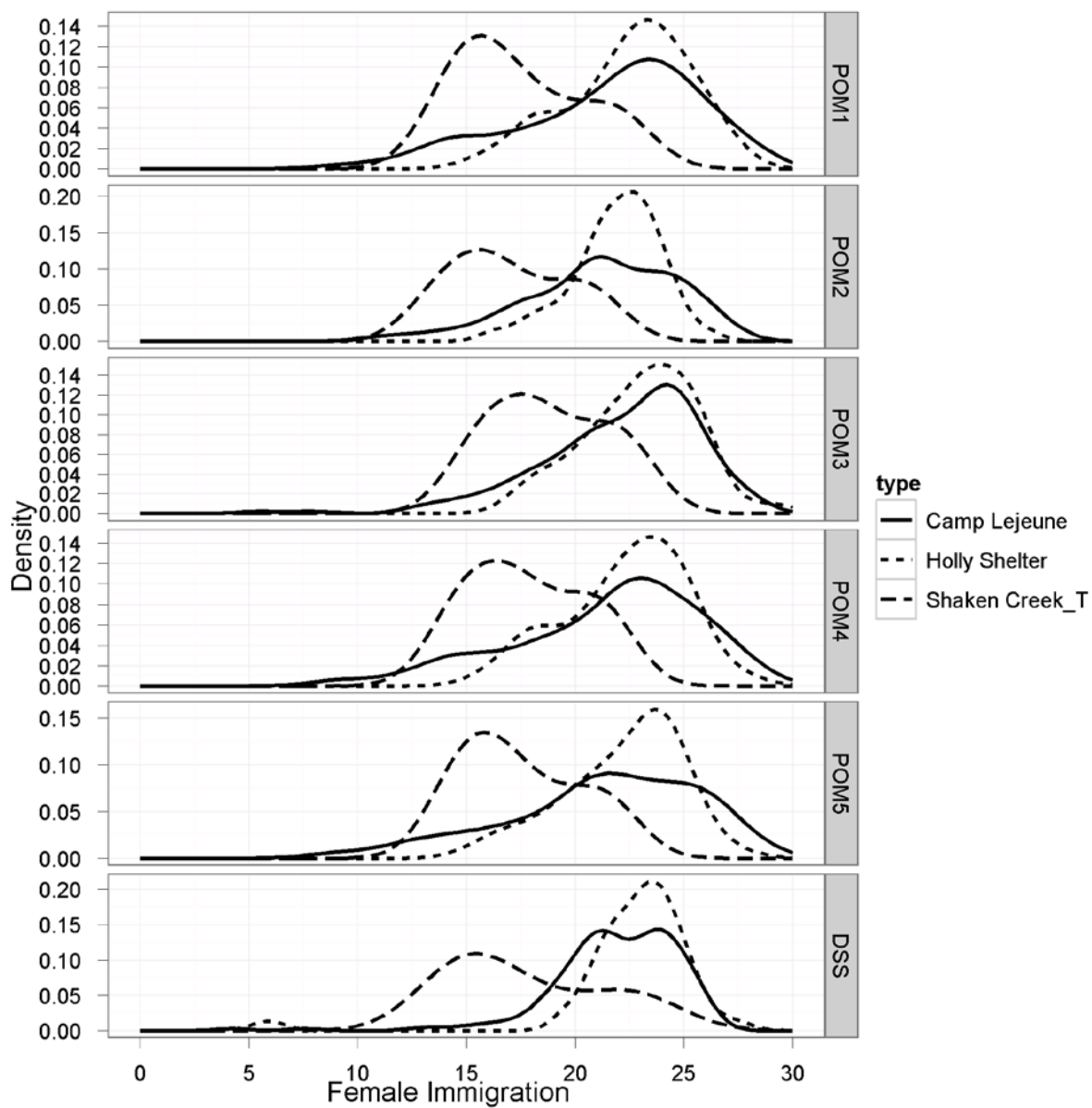


Figure B26. Distribution of patch-(territory-)based attributes summarized by property for total number of female migrants received by a patch.

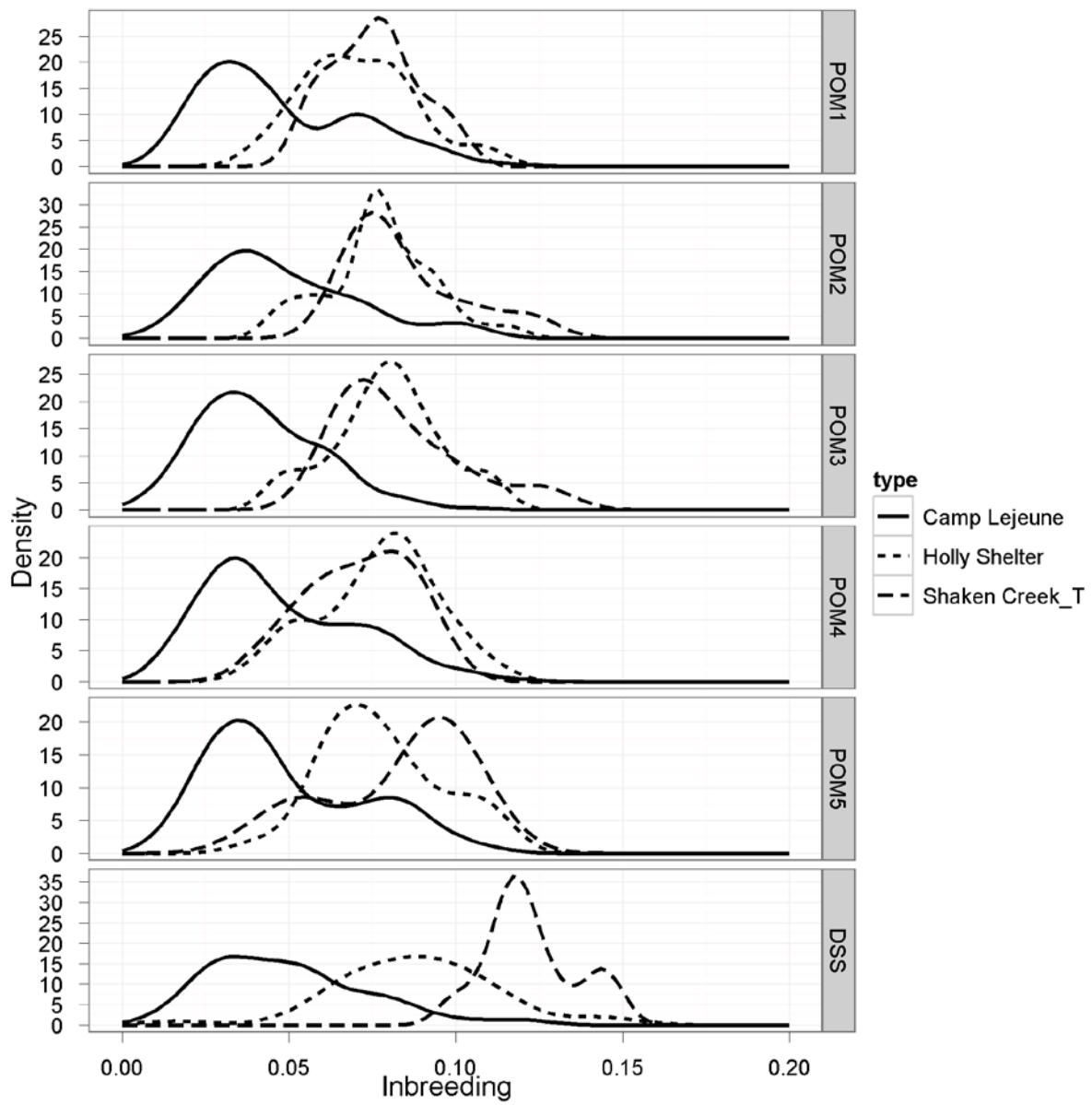


Figure B27. Distribution of patch-(territory-)based attributes summarized by property for Wright's Inbreeding coefficient at year 100.

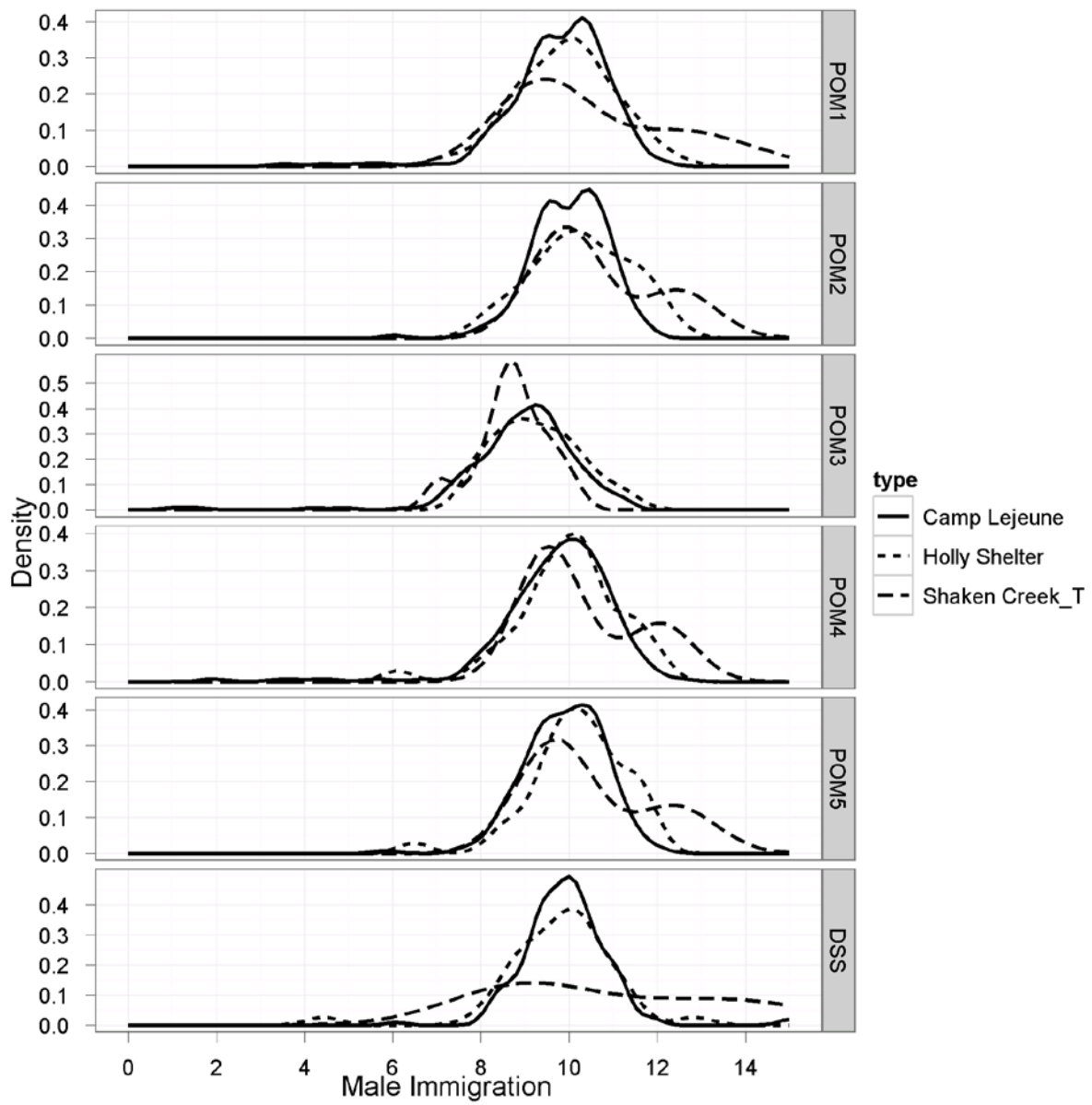


Figure B28. Distribution of patch-(territory-)based attributes summarized by property for total number of male migrants received by a patch.

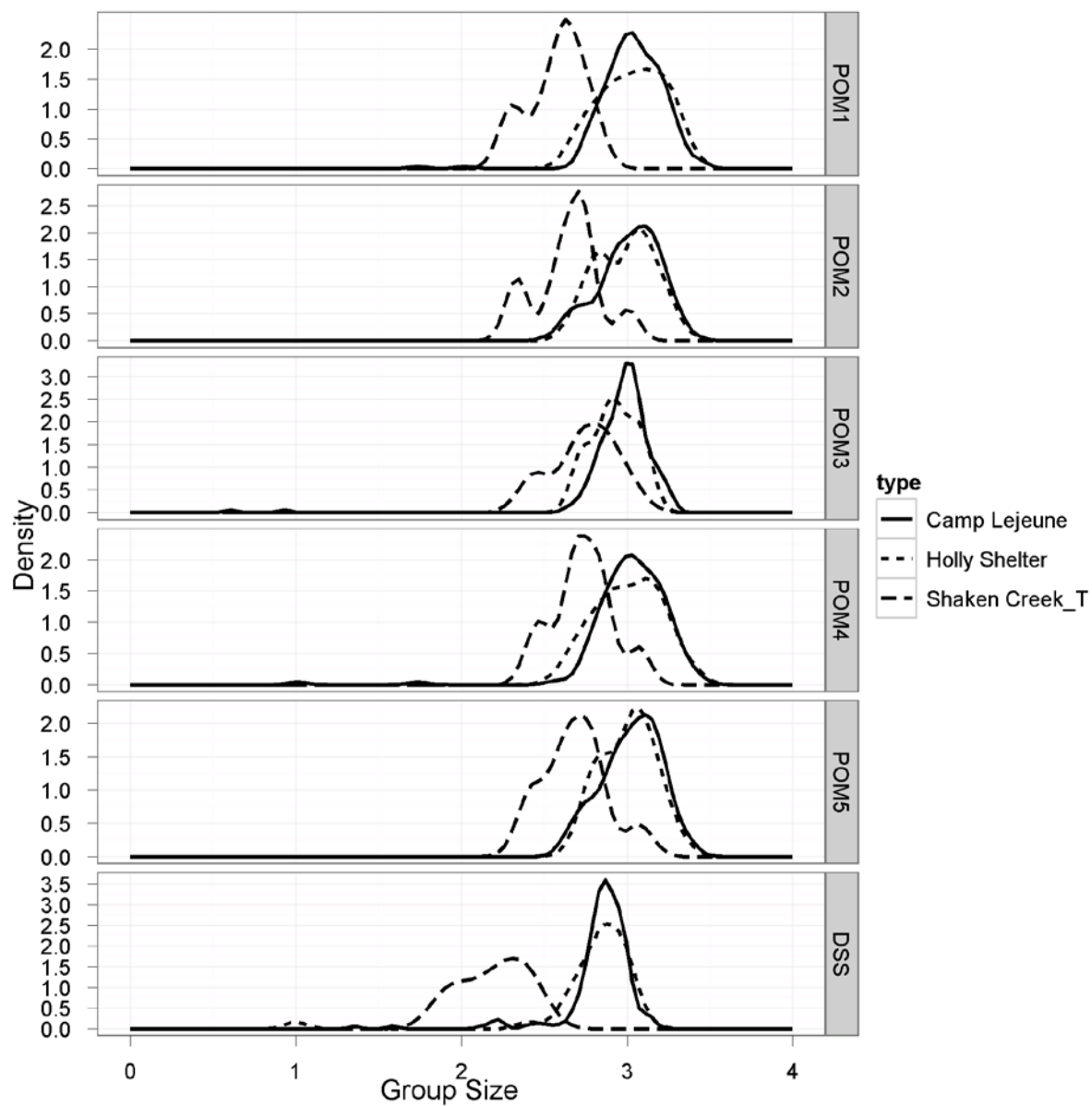


Figure B29. Distribution of patch-(territory-)based attributes summarized by property for group size (number of breeders and helpers) averaged over the number of years the patch was available for occupancy

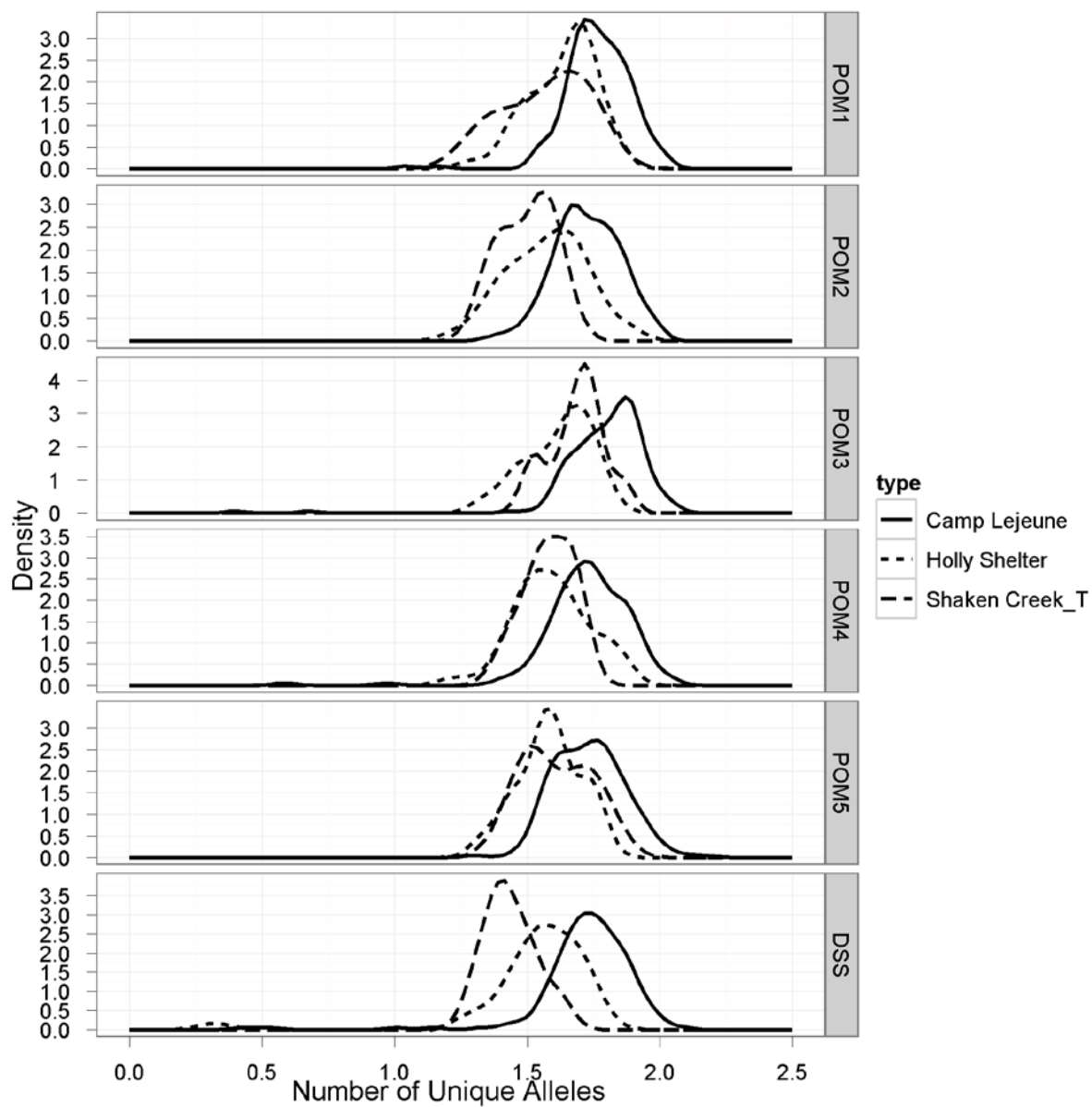


Figure B30. Distribution of patch-(territory-)based attributes summarized by property for number of unique alleles at locus 2 (sd = 1.0) at year 100.

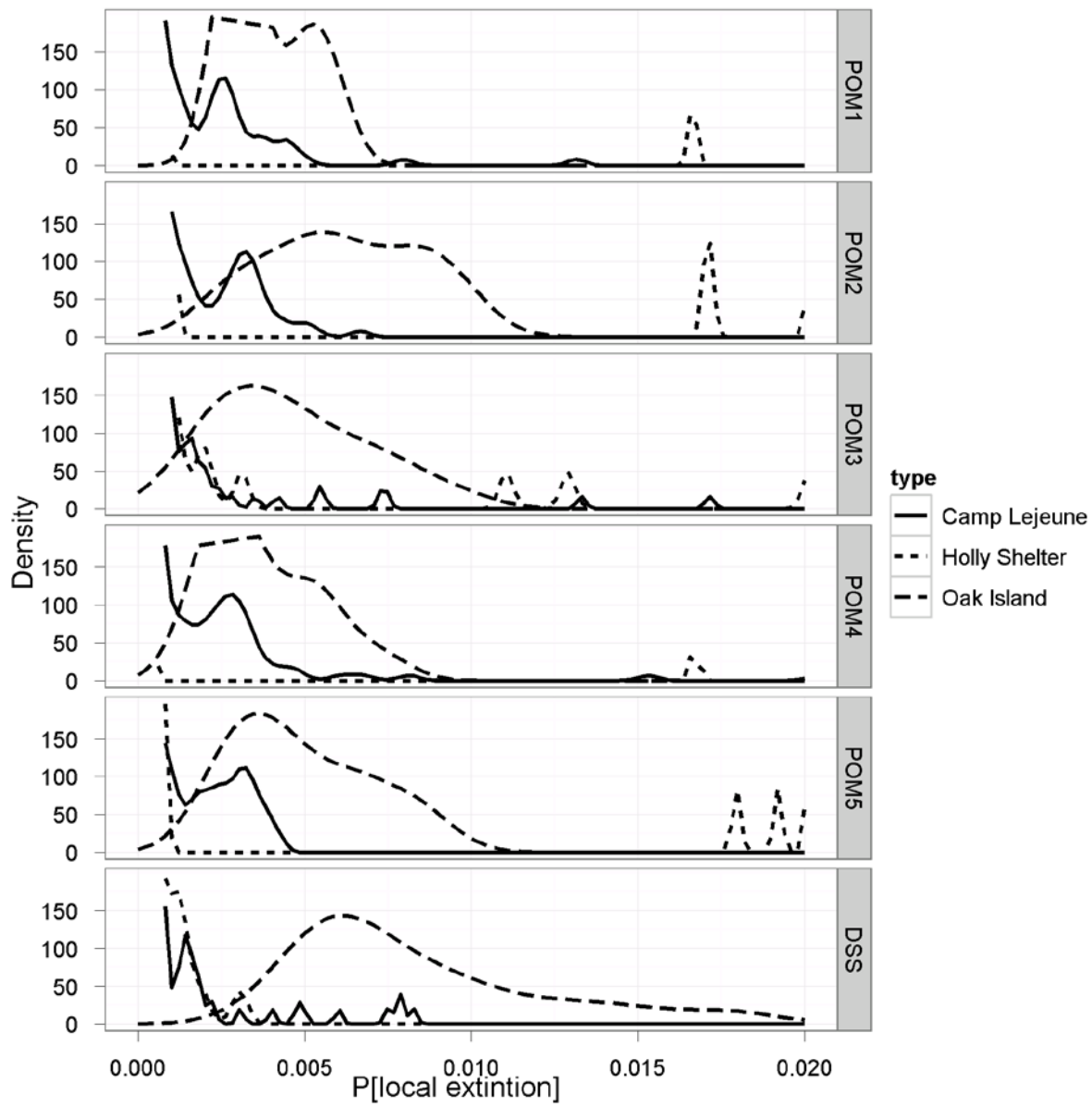


Figure B31. Distribution of patch-(territory-)based attributes summarized by property for probability of local extinction averaged over the number of years the patch was available for occupancy.

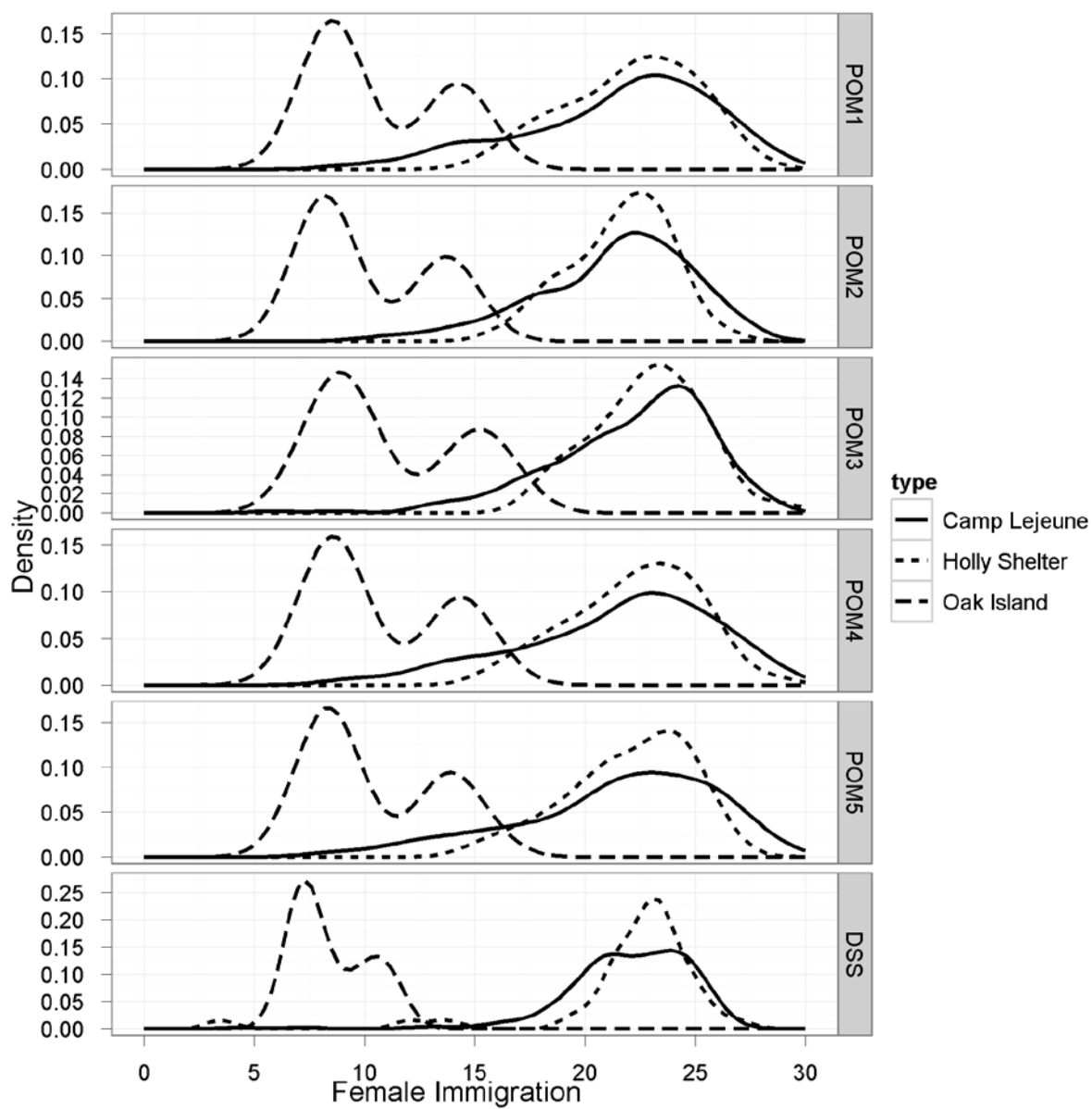


Figure B32. Distribution of patch-(territory-)based attributes summarized by property for total number of female migrants received by a patch.

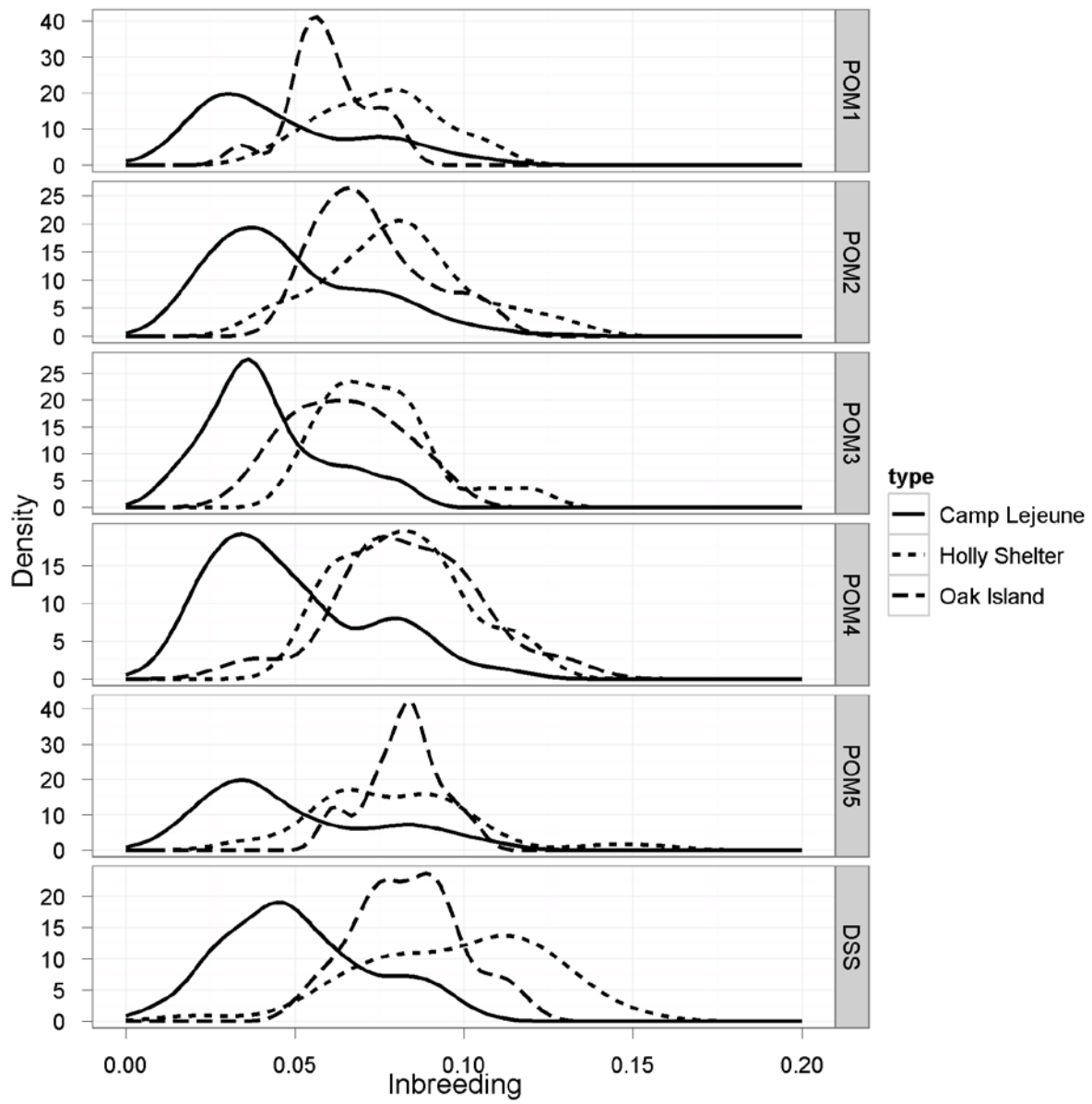


Figure B33. Distribution of patch-(territory-)based attributes summarized by property for Wright's Inbreeding coefficient at year 100

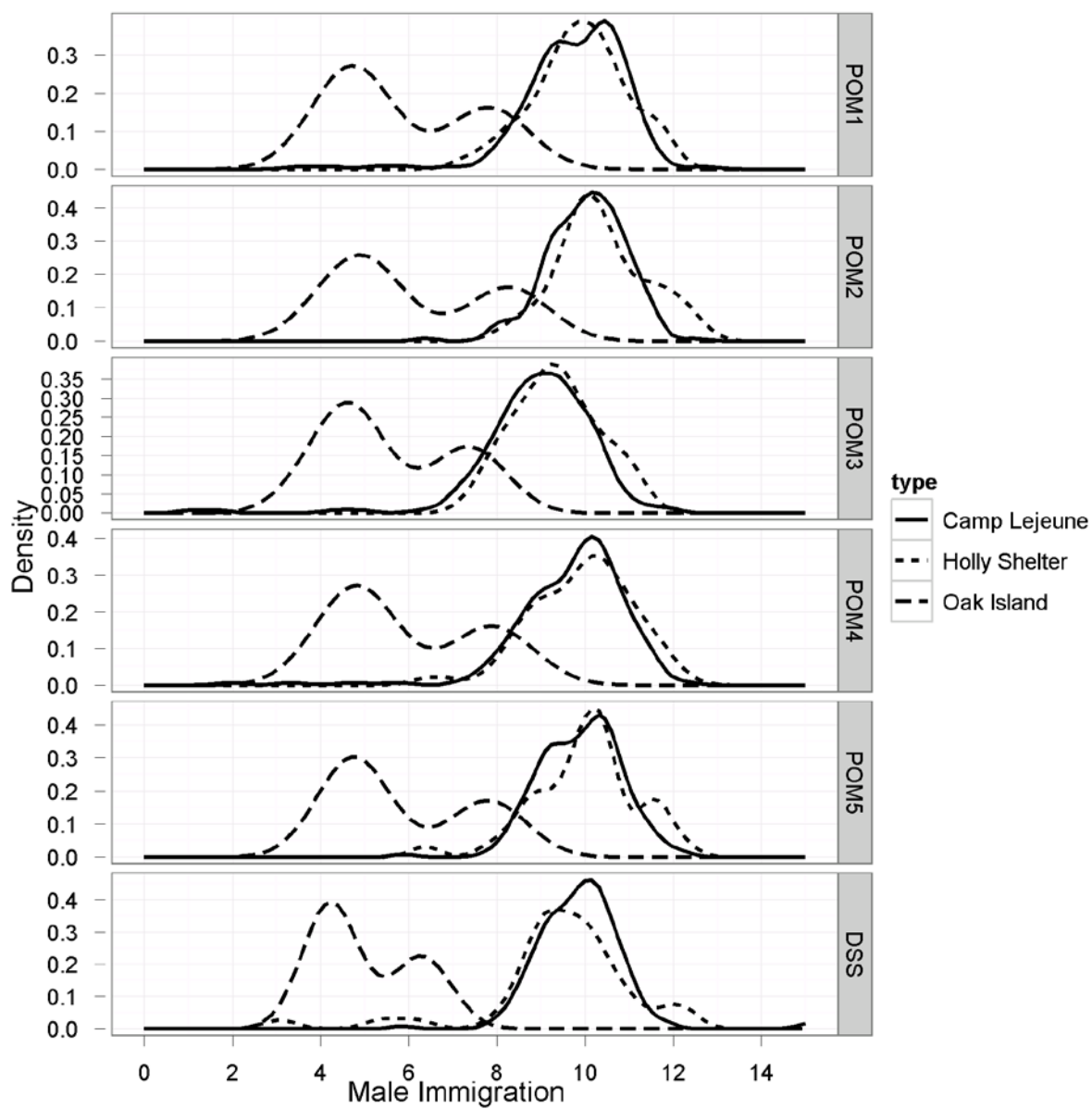


Figure B34. Distribution of patch-(territory-)based attributes summarized by property for total number of male migrants received by a patch.

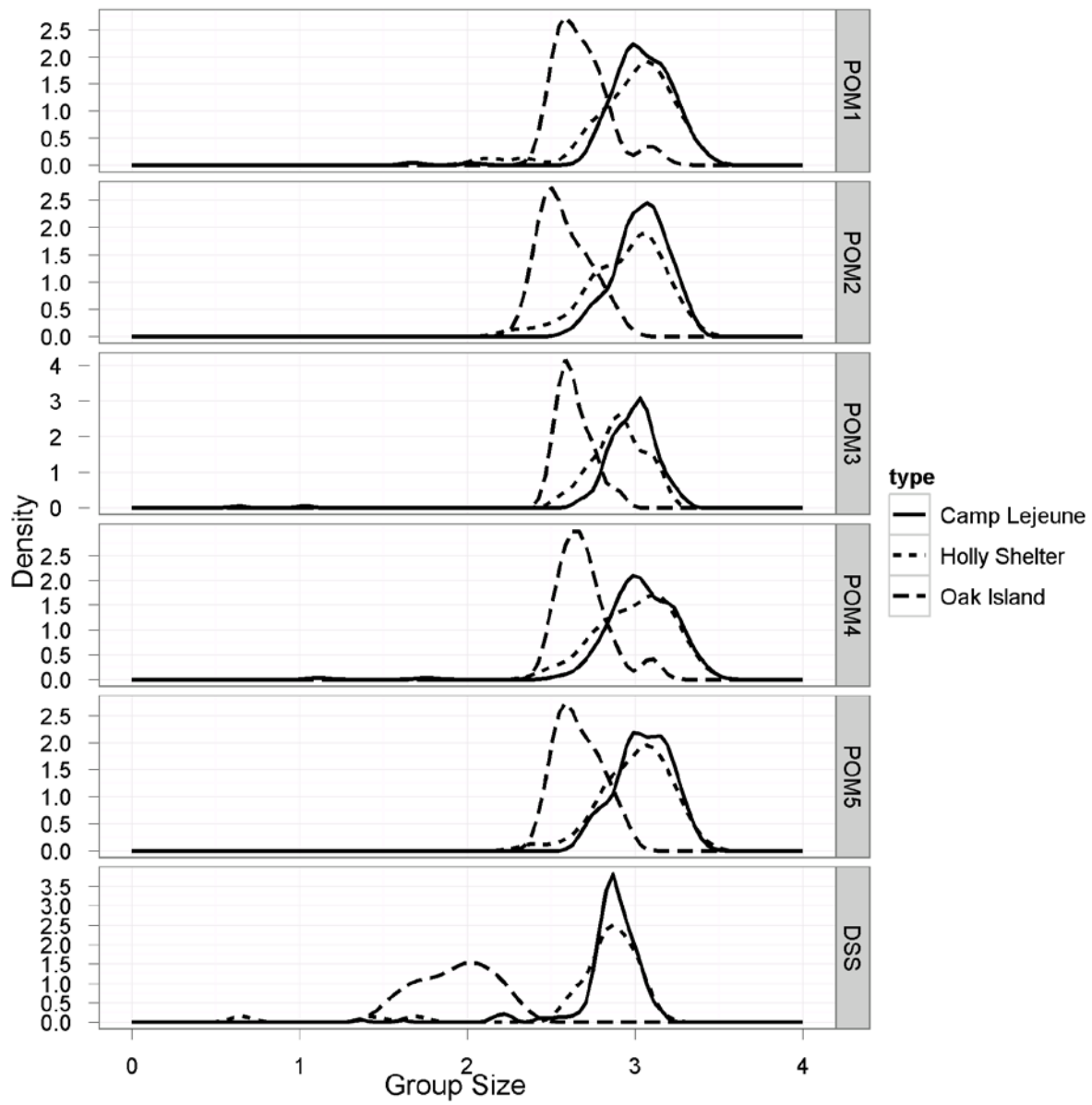


Figure B35. Distribution of patch-(territory-)based attributes summarized by property for group size (number of breeders and helpers) averaged over the number of years the patch was available for occupancy

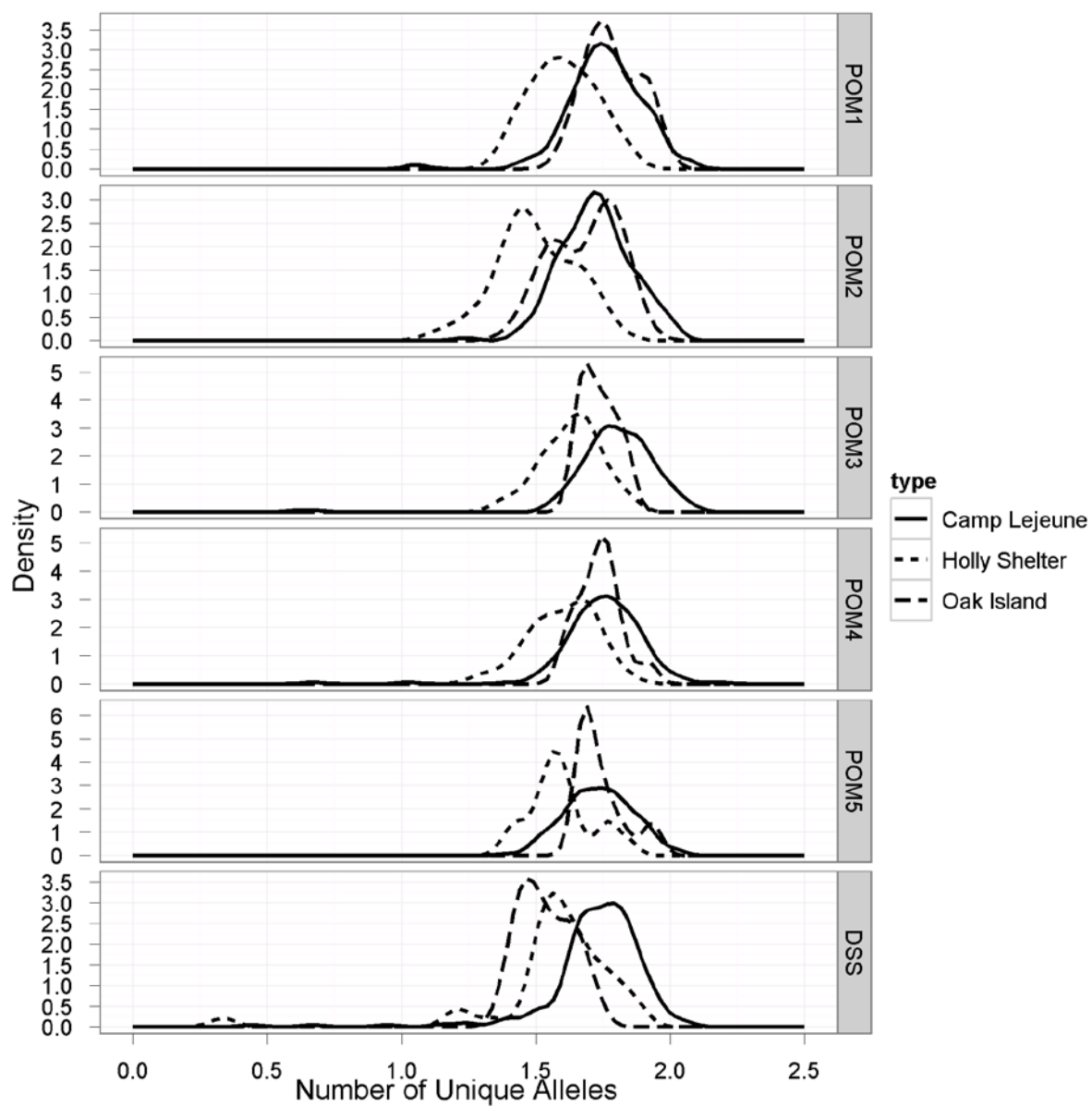


Figure B36. Distribution of patch-(territory-)based attributes summarized by property for number of unique alleles at locus 2 (sd = 1.0) at year 100.

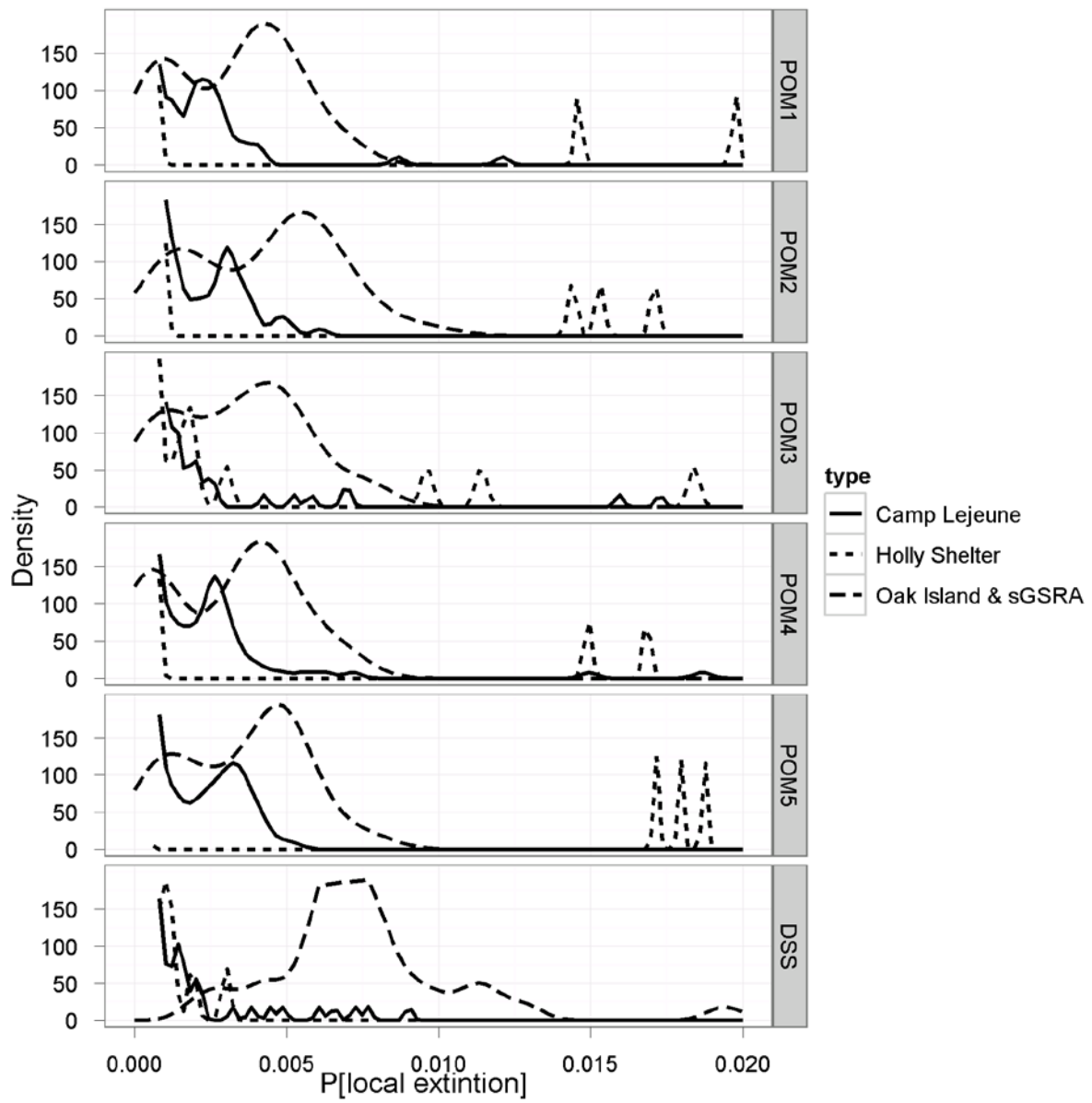


Figure B37. Distribution of patch-(territory)-based attributes summarized by property for probability of local extinction averaged over the number of years the patch was available for occupancy.

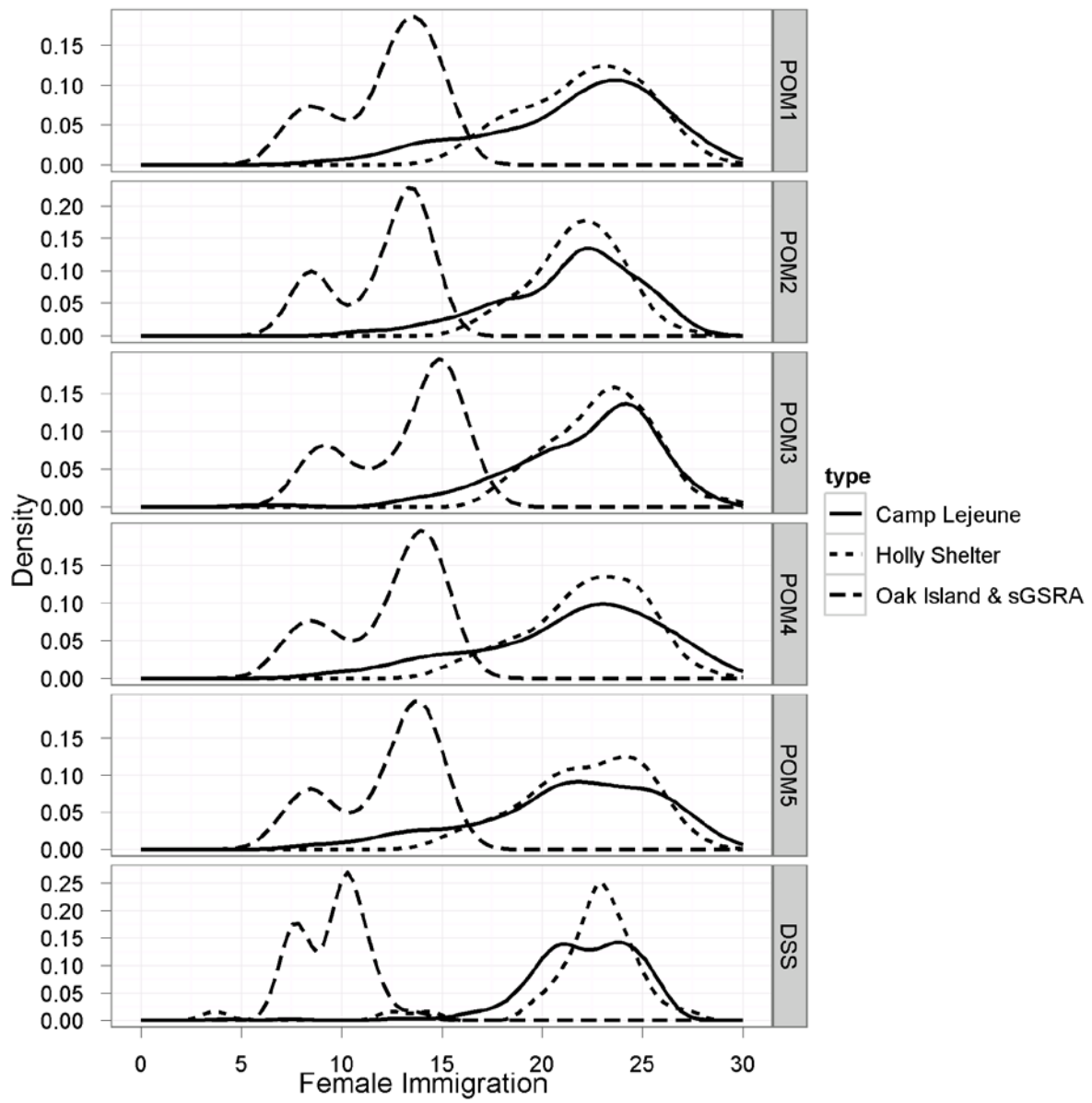


Figure B38. Distribution of patch-(territory-)based attributes summarized by property for total number of female migrants received by a patch.

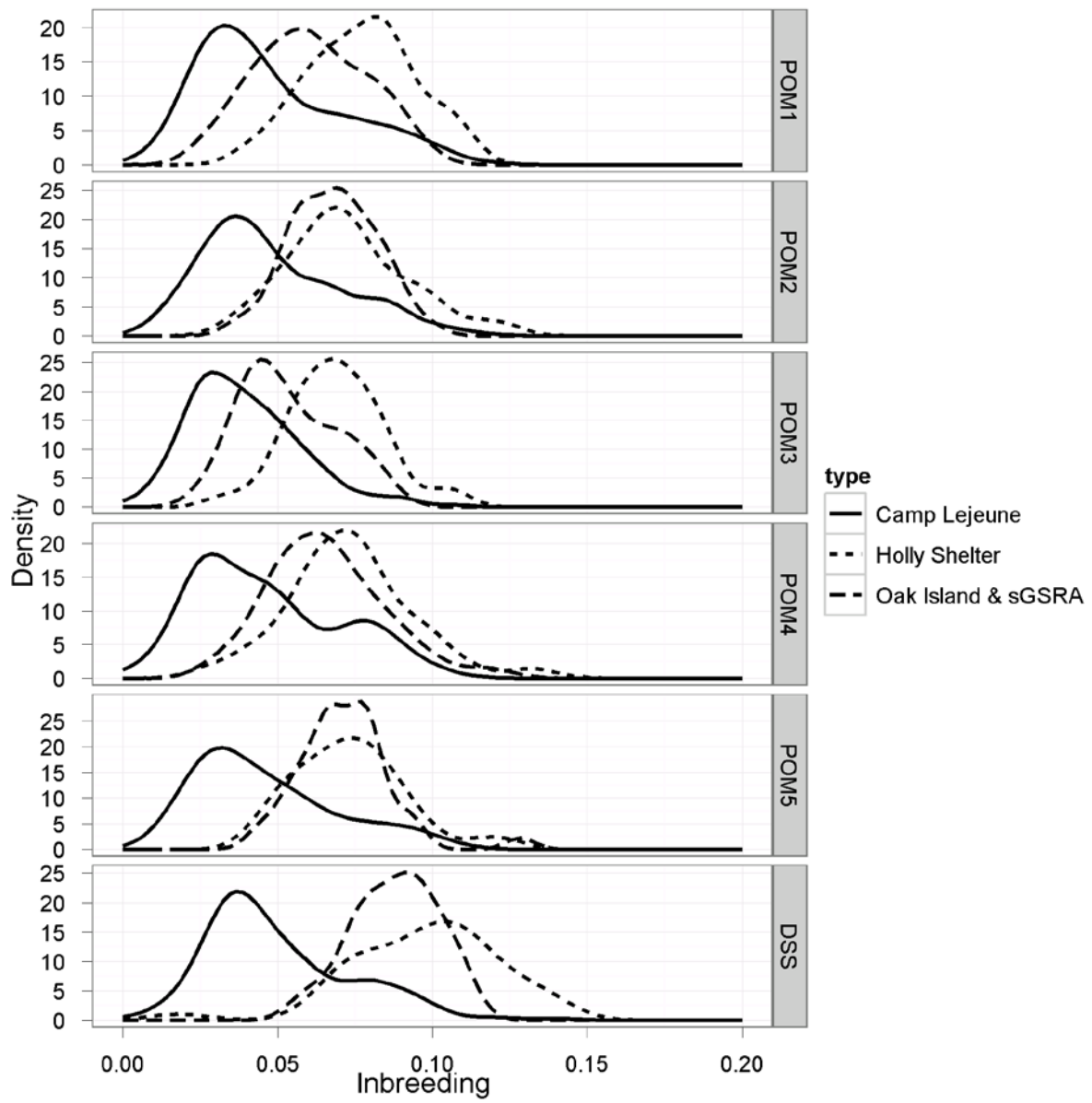


Figure B39. Distribution of patch-(territory-)based attributes summarized by property for Wright's Inbreeding coefficient at year 100.

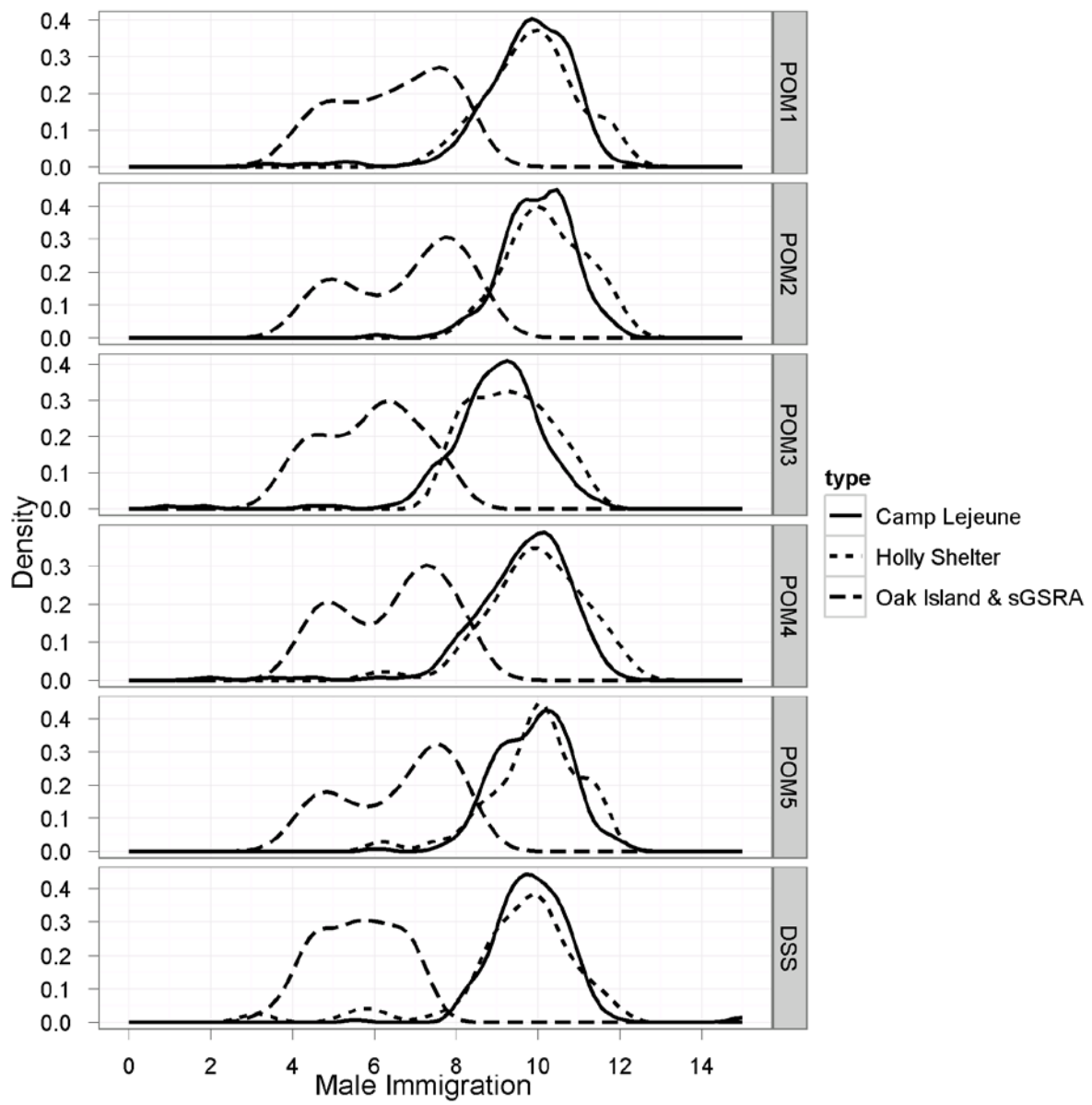


Figure B40. Distribution of patch-(territory-)based attributes summarized by property for total number of male migrants received by a patch.

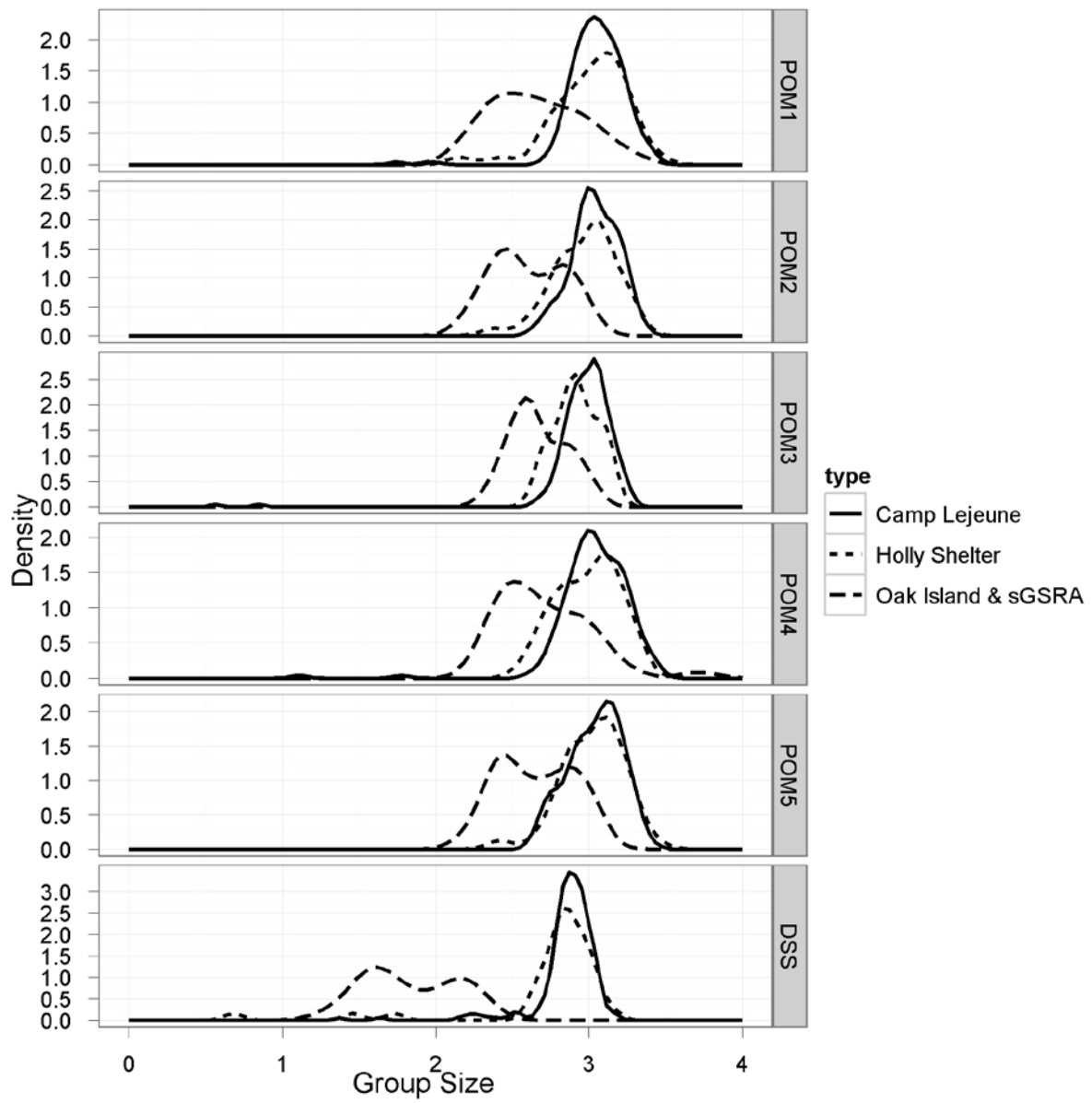


Figure B41. Distribution of patch-(territory-)based attributes summarized by property for group size (number of breeders and helpers) averaged over the number of years the patch was available for occupancy

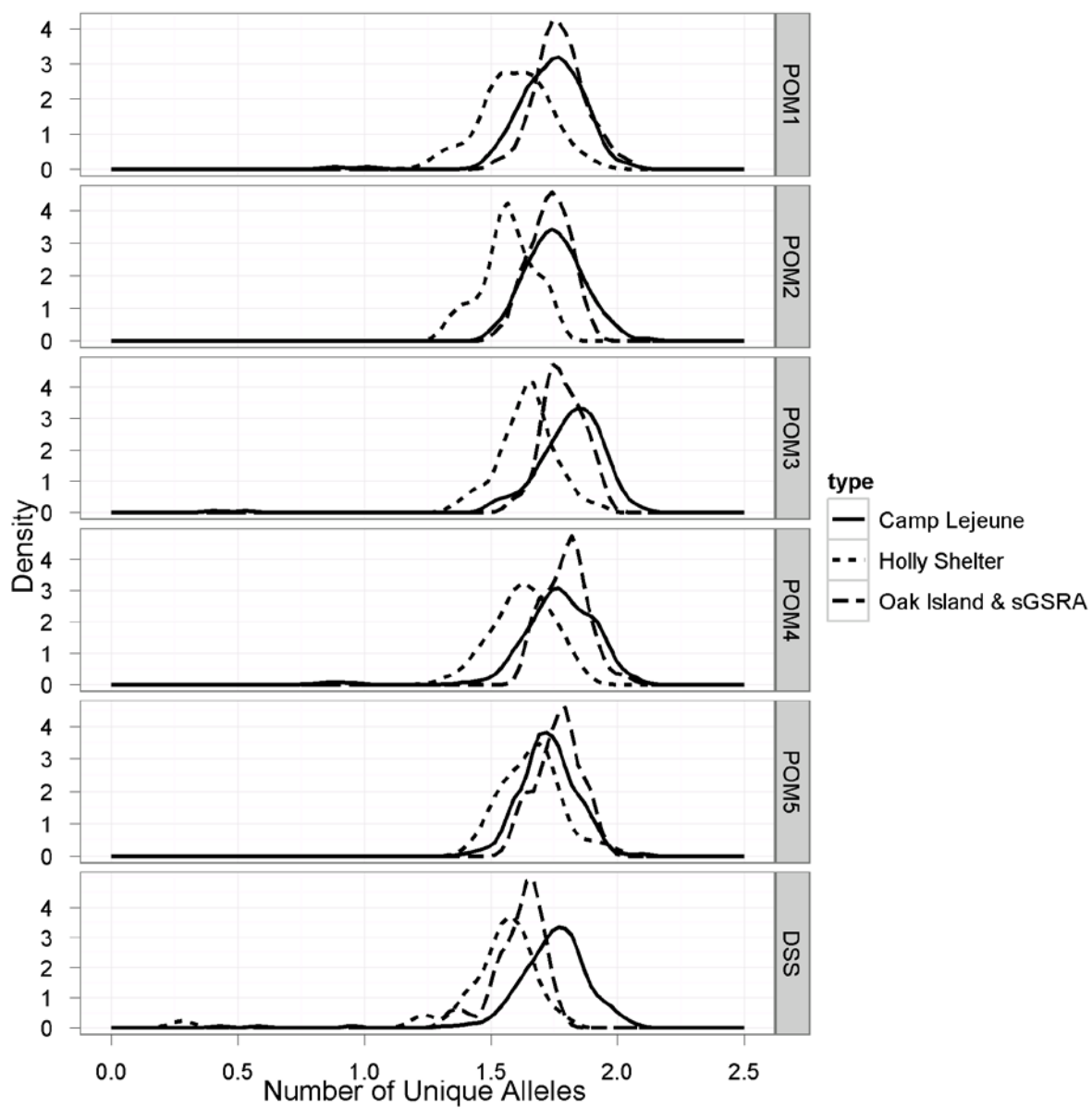


Figure B42. Distribution of patch-(territory-)based attributes summarized by property for number of unique alleles at locus 2 ($sd = 1.0$) at year 100.

APPENDIX C: DESCRIPTION OF THE INDIVIDUAL-BASED, SPATIALLY EXPLICIT POPULATION MODEL FOR GOPHER TORTOISE

Details of the gopher tortoise IB-SEPM are described below following the Overview, Design concepts, and Details (ODD) protocol, which is intended to provide a standard approach for describing agent-based models across studies to increase transparency (Grimm et al. 2010).

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1. PURPOSE

The objective of the model is to simulate life history traits of gopher tortoise (*Gopherus polyphemus*) populations to gain a better understanding of how the species may persist under different habitat management decisions and landscape compositions. There is much uncertainty regarding how the survival, reproduction and dispersal of tortoises are affected by landscape patterns. The objective of this model is to compile relevant biological mechanisms that describe the species natural history, identify critical areas of uncertainty, and determine how this uncertainty affects our ability to make management decisions.

The model is specifically developed for the military installation Ft. Benning (FB), which lies across three counties in Georgia and Alabama, USA. Relocations of tortoises within and beyond the installation are planned as an offset or, perhaps, banking strategy. However, it remains unclear under how well and under what conditions relocations can contribute to the long term persistence of the population. The strength of the approach that we take here is modeling of individual behaviors that are important for the long-term viability of a tortoise population, including movement and mating opportunities. The model will be used to choose suitable habitat for the relocation of gopher tortoises around FB, making use of the best available knowledge about tortoise behavior and natural history.

2. ENTITIES, STATE VARIABLES, AND SCALES

Tortoises. The basic entity of the model is a tortoise. Each tortoise is characterized by a unique ID, age, sex, natal location, current location, lifestage (determined by age), genetic configuration, home range (adults only), and sperm storage (adult females only).

Burrows: Gopher tortoises spend approximately 90% of their time in burrows that they dig in the ground (Eubanks et al. 2003), and gopher tortoise surveys focus on burrow locations (Nomani et al. 2008, Smith et al. 2009). Therefore the location of adult tortoises in the simulation is represented by the burrows of their home range, and for immature tortoises their natal burrow (i.e., nest site). Each burrow is associated with a location (x, y coordinates specifying the containing grid cell), activity (active or abandoned), last year occupied, and occupying tortoises.

Landscape: The landscape of the simulation encompasses the outlines of FB (approximately 73,800 ha), potential Army Compatible Use Buffer (ACUB) properties (40,800 ha), and a 12 km buffer around the combined areas (Figure C1). The total area of the landscape is 346,000 ha. The landscape is modeled as a static grid of 30 m x 30 m grid cells, where each grid cell is associated with a habitat suitability value. Habitat suitability values

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were calculated with a logistic resource selection probability function (RSPF; Lele and Keim 2006, Lele et al. 2011), which describes the probability of burrow presence as a linear combination of environmental variables. The RSPF combined important environmental variables (described in detail in Kowal et al. in review, and outlined in Table C1 below) at each grid cell location to predict the suitability for burrow establishment in the grid cell.

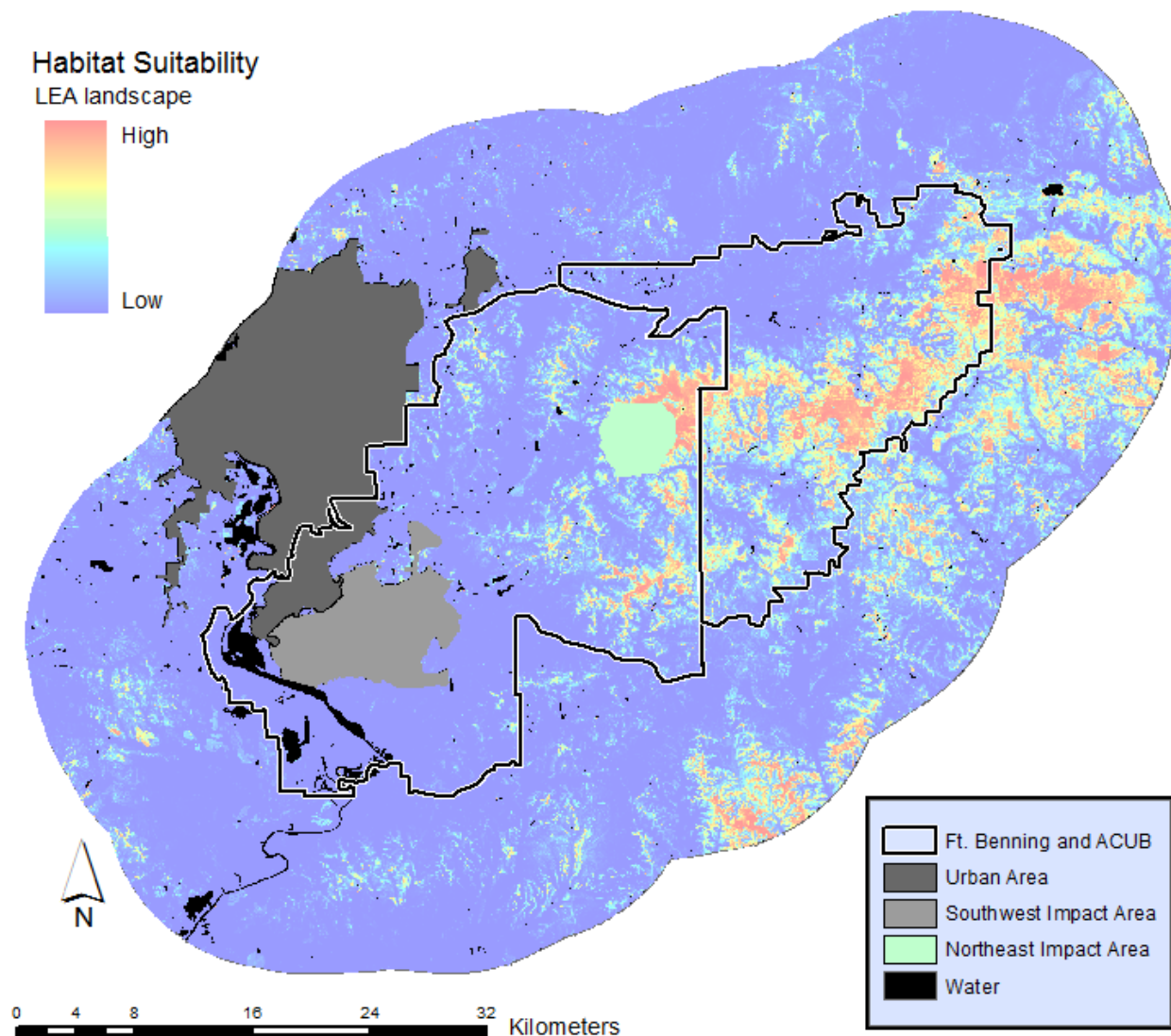


Figure C1. The simulation landscape, showing boundaries of Ft. Benning (southwestern property) and ACUB (adjacent northeastern property). Habitat suitability values shown are from the global habitat model (defined below; and used for LEA); the overall distribution of habitat on the POM and pre-settlement landscapes is similar.

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Table C1. Environmental datasets used to derive the habitat suitability landscape grid for each simulation mode.

Environmental variable	Source
Topography	Calculated from Digital Elevation Model
Elevation (m)	
Slope (%)	
Soil	Calculated from SSURGO soils database
Sand in top 1 m (%)	
Soil drainage index (ordinal variable)	
Landscape Features	Landsat 5 Thematic Mapper, 2007
Distance to water (m)	
Distance to paved roads (m)	
Vegetation Density	Landsat 5 Thematic Mapper, 2008 and 2009
Winter NDVI	
Difference between winter and summer NDVI	

The coverage of the habitat suitability model is limited by the availability of soil survey data (Figure C1). Two large impact areas in the interior of FB contain unexploded artillery and are not included in soil surveys. One of these impact areas, the Northeast (NE) impact area, is of high habitat quality and contains a large number of unsurveyed gopher tortoise burrows (Mark Thornton, Ft. Benning, personal communication). We include this impact area in the simulation by treating it as an area of homogeneous habitat quality equal to the average of suitability values in cells bordering the impact area (0.334 for the POM landscape; 0.379 for the LEA landscape; 0.486 for the pre-settlement landscape).

The second impact area is known to be of low habitat quality, and in the simulation is assumed to have uniform suitability of zero. Because tortoises are not known to inhabit developed areas (Hermann et al. 2002, Baskaran et al. 2006), urban areas within the city limits of Columbus, which is adjacent to FB, are also assumed to have a habitat suitability value of zero (Figure C1). Other small areas where soil survey coverage is unavailable include streams and waterbodies. Tortoises are allowed to traverse water features in the simulation but may not establish burrows there (see Emigration submodel, Section 7).

Habitat suitability values are invoked when tortoises dig new burrows, where they are restricted to add burrows in areas above a threshold suitability value. This threshold value is defined for each landscape from the distribution of habitat values in grid cells containing surveyed burrows. An important exception to this restriction is that when emigrating tortoises end their emigration path in an area of low habitat quality, they are

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allowed to dig burrows there (details in Emigration submodel, Section 7). Tortoise emigration paths are also informed by habitat (see Emigration submodel), where suitability is interpreted as the permeability of the landscape to movement.

We developed separate habitat suitability models for the POM simulation and the LEA simulation, depending on the availability of datasets that reflected environmental conditions during the time frame over which each simulation experiment was run. Before evaluating the fit of the two RSPF models, we performed a variable elimination procedure by first calculating Spearman rank correlations of all environmental variables included in the model and, when two or more variables were highly correlated ($\rho > 0.7$), removing the variable with weakest bivariate support. We then calculated variance inflation factors (VIF) for each suitability model and when two or more variables showed VIF greater than 3, we eliminated one variable with weakest bivariate support.

The method by which we evaluated the two habitat models is described in detail in Kowal et al. (in review); we briefly outline the process here. We compared the ability of the two models to explain observed burrow locations from a 2008-2010 burrow survey of FB using Akaike's Information Criterion (AIC), the area under the curve (AUC), and ten-fold cross-validation (CV). The AUC statistic describes the ability of a model to discriminate recorded presences from recorded absences (Fielding and Bell 1997). AUC values range from 0 to 1; a value of 0.5 indicates a model that classifies cases randomly, while a value of 1 indicates a model that correctly classifies all cases (Fawcett 2006). Cross-validation is a complementary analysis to AIC and AUC and assesses the accuracy of a predictive model (Stone 1977). In this method, the dataset is divided into 10 random subsets and each of the subsets is used once for testing, while the remaining nine subsets are used for model fitting. We used the "DAAG" package in R (Maindonald and Braun 2012) to calculate the average percent of correctly predicted cases over 20 iterations of cross-validation. These analyses together showed that a global model including all available environmental variables was superior to an abiotic model that excluded variables describing vegetation (Global AIC 32718; AUC 0.905; CV 84%, Abiotic AIC 33634; AUC 0.879; CV 82%).

POM landscape. The habitat suitability model employed for the shortPOM simulation experiment is derived from data that were available for the time period over which POM simulations are run (1999 – 2009). The best fit for the habitat model included vegetation data from 2008 and 2009 (Table C2), but because vegetation density in the longleaf pine community can change quickly (Aresco and Guyer 1999), we omitted all vegetation data from the landscape used for POM. Therefore suitability values on the POM landscape were calculated from variables describing topography, soil, and distance to landscape features only (i.e., an abiotic model; Table C2). The model predicts high suitability for gopher tortoise burrows in areas of high elevation and little slope, at distance from paved roads, and in sandy soils with low long-term wetness (Table C2). The median suitability value in cells where surveyed burrows were present on the shortPOM landscape was 0.323; this is the threshold

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habitat suitability value that is applied during the shortPOM experiment when tortoises dig new burrows.

LEA landscape. The habitat model employed for the LEA approach was the model with the best fit, or the global model, which includes variables describing topography, soil, distance to landscape features, and vegetation density (Table C2). Vegetation density included in the model was estimated from remote sensing data captured by the Landsat 5 Thematic Mapper in 2008 and 2009, coinciding with the collection of the burrow survey used to initialize the LEA simulation. To capture both the primarily deciduous and non-deciduous fractions of vegetation on FB, we calculated winter Normalized Difference Vegetation Index (NDVI; which primarily reflects evergreen vegetation) and the difference between winter and summer NDVI, NDVI difference (which is strongly associated with hardwood basal area and midstory vegetation, Kowal et al. in review). The global model predicts high suitability for gopher tortoise burrows in areas with sandy, well-drained soils, low deciduous and evergreen vegetation density, at distance to paved roads and water bodies, and at high elevation with gentle slope (Table C2). The median suitability value in cells where surveyed burrows were present on the LEA landscape (i.e., the threshold habitat value where tortoises may dig new burrows) was 0.551.

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Table C2. Summary of resource selection probability function models for gopher tortoise habitat suitability on Ft. Benning, Georgia. The global model that includes all available environmental variables was superior to an abiotic model that does not include vegetation (Global AIC 32718; AUC 0.905; CV 84%, Abiotic AIC 33634; AUC 0.879; CV 82%).

Covariate	Estimate	SE	z	p
Abiotic model				
Intercept	-10.79	0.35	-30.67	< 0.001
Elevation	0.04	0.001	26.97	< 0.001
Slope	-0.20	0.01	-17.84	< 0.001
Distance to paved roads	0.0004	0.00002	17.15	< 0.001
% Sand in top 1 m	0.06	0.004	14.49	< 0.001
Soil drainage index	-0.03	0.003	-11.21	< 0.001
Distance to water	-0.00008	0.00003	-3.18	0.001
Global model				
Intercept	-7.53	0.20	-37.35	< 0.001
% Sand in top 1 m	0.06	0.001	39.99	< 0.001
NDVI difference	-6.99	0.29	-24.19	< 0.001
Distance to paved roads	0.0005	0.00002	23.40	< 0.001
Winter NDVI	-4.77	0.21	-22.84	< 0.001
Elevation	0.02	0.001	20.94	< 0.001
Soil drainage index	-0.02	0.002	-11.99	< 0.001
Distance to water	0.0004	0.00004	9.52	< 0.001
Slope	-0.09	0.02	-6.04	< 0.001

Pre-settlement landscape. The pre-settlement landscape approximates the historical distribution of habitat on FB prior to the arrival of European settlers. While quantitative data describing ancestral vegetation on FB are not available, historical accounts suggest that the installation was dominated by the longleaf pine grassland ecosystem (Frost 1993). In the absence of vegetation data for this time period, we reconstructed the pre-settlement landscape by first estimating abiotic habitat suitability. The pre-settlement habitat suitability model incorporated only topography, soil, and distance to waterbodies (i.e., those aspects of the global model that are not expected to have been affected by human activities, Table C1). We then accounted for expected high quality of the ancestral vegetation by estimating an increased density of burrows over that which is observed on the installation today, as described under burrow pattern prediction (Section 5B). After burrow locations were estimated with burrow reconstruction, the median suitability value in cells where estimated burrows were located was 0.678.

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Time

POM Approach. The shortPOM simulation experiment is initialized at year 1999 and run to 2009, because empirical data are available for model initialization in 1999 and for estimating errors in model predictions in 2009. A single time step of the model represents one year.

In contrast, for the longPOM experiment we simulated the demographic history of the region starting prior to settlement by Europeans. The objective of the longPOM experiment is to include estimates of errors in model fit associated with both genetic and demographic data observed on FB from the 2008-2010 time frame (i.e., the time at which observed data describing burrow patterns and population genetics were available). The genetic and demographic structure of the extant population within the boundaries of FB was likely affected by land use change occurring within FB current boundaries and the area to the northeast along the Chattahoochee Fall Line. Therefore, to simulate the impacts of European settlement and subsequent restoration of FB, we structured the longPOM simulation experiment with four time intervals over which various rates of demographic decline and recovery are applied (Table C3).

The first interval simulates 500 years of pre-settlement (or baseline) conditions prior to substantial impacts by Europeans in the region. Nest predation rate during this period is decreased relative to present-day levels, reflecting our expectation that predation of gopher tortoise nests has increased with regional urbanization and the establishment of non-native predators (Smith et al. 2013). We identified this baseline nest predation rate by identifying the rate that would allow for stable population growth (i.e., $\lambda = 1$) given all other demographic parameters (parameter values and sources listed in Table C6), giving a “baseline” nest predation rate of 0.648 compared to the current estimated (status quo) nest predation rate of 0.71.

The second interval, from 1827 to 1880, represents a slow decline in the population caused by slowly increasing adult and subadult mortality that was expected to accompany beginning impacts of Europeans. Nest predation remains unchanged during this second interval. The third interval, from 1881 to 1950, sees a drastic decline in the tortoise population with quickly increasing adult and subadult mortality that is expected to have occurred during major forestry and agricultural activity in the region (nest predation during this interval remains unchanged). In the fourth interval, from 1951 to 2009, adult mortality on FB returns to current observed levels, reflecting reforestation and protection of tortoises on the installation. At the same time, nest predation during the fourth interval increases from estimated pre-settlement levels to those that are observed in the field today, or status quo. Outside the boundaries of FB, during the fourth interval the remaining tortoises continue to experience increasing adult mortality and increasing nest predation. This reflects our expectation of drastic population declines due to lack of protection outside of FB. The demographic decline of the population was

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calibrated so that the size of the tortoise population inside FB at year 1999 would approximate the number suggested by the 1999 burrow survey.

Table C3. Intervals implemented for the longPOM experiment.

Interval	Starting year	Ending year	Adult and subadult mortality		Nest predation	
			Inside FB	Outside FB	Inside FB	Outside FB
1	1326	1826	baseline	baseline	baseline	baseline
2	1827	1880	slow increase	slow increase	baseline	baseline
3	1881	1950	fast increase	fast increase	baseline	baseline
4	1951	2009	baseline	fast increase	status quo	status quo

LEA Approach. The LEA simulation experiment is initialized at year 2009 and run to 2108. Again, a single time step of the model represents one year.

3. PROCESS OVERVIEW AND SCHEDULING

Pseudocode of the schedule during each time model run is provided below.

<p><i>POM Approach:</i></p> <p>Read data files (parameter values, landscape grids, burrow survey)</p> <p>For parameterization p</p> <p> For Monte Carlo m</p> <p> Initialize tortoise population</p> <p> For year t = 1999 to 2009</p> <p> Mortality</p> <p> Update burrows</p> <p> Aging</p> <p> Emigration</p> <p> Assign female home range</p> <p> Assign male home range</p> <p> Reproduction</p> <p> Population census</p> <p> Population genetic statistics</p> <p> End t [year]</p> <p> End m</p> <p>Estimate fit using sums of squares</p> <p>End p</p>	<p><i>LEA Approach:</i></p> <p>Read data files (parameter values, landscape grids, burrow survey)</p> <p>For parameterization p</p> <p> For Monte Carlo m</p> <p> For Land L</p> <p> Initialize tortoise population</p> <p> For year t = 2009 to 2108</p> <p> Mortality</p> <p> Update burrows</p> <p> Aging</p> <p> Emigration</p> <p> Assign female home range</p> <p> Assign male home range</p> <p> Reproduction</p> <p> Population census</p> <p> Population genetic statistics</p> <p> if t = 2029</p> <p> Remove habitat</p> <p> Relocate tortoises</p> <p> End t [year]</p> <p> End L</p> <p> End m</p> <p>Collect landscape-scale data for LEA</p> <p>End p</p>
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4. DESIGN CONCEPTS

The basic principles underlying the model's design are the associations between demographic and genetic components of population structure in a dynamic landscape. Individuals in the model are responsive to both surrounding landscape characteristics and to each other. The space use and movement by individuals affects population persistence and the distribution of individuals and genetic variance across the landscape.

4A. POM APPROACH

Initially, spatially explicit population models (SEPMs) were criticized due to their complexity, large data requirements, and use of uncertain parameter estimates (Beissinger and Westphal 1998). However, an approach called Pattern Oriented Modeling (POM) has been used to construct and validate SEPMs with less data than previously imagined (Wiegand et al. 2004, Grimm et al. 2005). Pattern Oriented Modeling is used to determine the model's ability to replicate complex patterns observed in nature. Therefore, the model is designed to compare summary statistics from the simulation to summary statistics that characterize actual populations, or

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observed patterns. The goal is then to minimize the deviation between the summary statistics of the observed and simulated patterns; i.e., the parameterization must be determined that minimizes the error functions.

4B. LEA APPROACH

Landscape Equivalency Analysis (LEA) is an extension of resource-based compensation applied to a landscape scale (Bruggeman et al. 2005). Resource-based compensation determines the amount of restoration required to equate an individual's well-being before loss of an ecological resource with their well-being after that loss (Jones and Pease 1997). A "service-to-service" approach is used wherein adequate compensation is made to the public if the habitats restored provide equivalent types and levels of ecological services as the habitats lost. Ecological functions can be treated as goods and services when a direct or indirect benefit to humans can be demonstrated (de Groot et al. 2002). In this analysis we assume that the ecological services that provide these benefits are abundance and genetic variance (Loomis and White 1996, Bruggeman et al. 2005). LEA estimates the equivalency of habitat patches traded in a fragmented landscape for gopher tortoises based on changes in two ecological services, abundance of adults and total expected heterozygosity (Nei 1973) measured at the landscape scale.

4C. GENERAL DESIGN CONCEPTS

Emergence: The home range of adults is constructed with an "energy budget" that limits the size of the home range in terms of the total pairwise distance between all burrows in the home range (see Assign home range submodels, Section 7). Although the energy budget itself is selected from an empirical distribution and enforced for each individual tortoise, the size of the home range and the number of burrows in the home range emerge from the interaction between the configuration of existing burrows and the energy budget allocated to the tortoise. Tortoise home ranges in turn give rise to other emergent properties such as number of sires of each clutch, paternity of each egg, and alleles possessed by new tortoises in the simulation. Higher-level emergent properties include the locations of tortoises and of burrows on the landscape, and the distribution of genetic variance across the landscape.

Objectives: The traits simulated allow males to seek mating opportunities with females by constructing home ranges that allow overlap with many female tortoises. Males and females also seek to avoid overlap with other members of the same sex when constructing their home ranges. When immature tortoises and adult females emigrate, they have the objective of ending their emigration path in an area of high habitat suitability.

Sensing: Tortoises are sensitive to habitat suitability during emigration and when they dig new burrows (see Emigration and Dig burrows submodels, Section 7). Adult male tortoises are also sensitive to the proximity of burrows occupied by females when emigrating (see Emigration submodel). Adult tortoises are responsive to the sex of other tortoises occupying a burrow when constructing their home range; see Assign home range

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submodels (Section 7).

Interaction: Adult tortoises interact via home range overlap, which dictates both mating encounters and avoidance of members of the same sex. Males and females can only mate if their home ranges overlap (see Reproduction submodel, Section 7). Immature tortoises do not participate in interactions.

Stochasticity: During the initialization procedure, stochasticity is included when determining the age distribution by comparing a $u[0,1]$ random number to a cumulative probability distribution to assign the age of each founder. Founding tortoises are also assigned a random initial location from among surveyed burrows. In the home range assignment submodel stochasticity is included in several ways. First, each year the home range is re-assigned starting from one burrow chosen at random from the previous year's home range (note that if the female burrow philopatry parameter is in effect this is not true for females; see Assign home range submodels, Section 7). The number of burrows in the home range is limited indirectly by an energy budget that is drawn at random from a sex-specific normal distribution. Burrows within increasing search radii are tested for inclusion in the home range in random order, and when a burrow is tested for inclusion, a random $u[0,1]$ number is compared to a fixed probability.

The emigration submodel includes stochasticity in the following ways: for adults, the starting grid cell for the emigration path is a burrow randomly chosen from the current home range. The number of steps that emigrants are assigned to undertake is drawn from a uniform distribution between sex- and lifestage-specific minimum and maximum values, and each step taken by the emigrant is determined by comparing a random $u[0,1]$ number to a cumulative probability distribution. When the tortoise finishes its emigration path, either because a stopping condition is met (see Emigration submodel, Section 7) or because it has reached the end of its allotted steps, a burrow chosen at random from those available within a radius is the first burrow added to the home range. If no burrows exist within that radius, the tortoise digs one or two burrows with equal probability (without regard to habitat suitability of the ending cell; see Emigration submodel).

Demographic submodels such as mortality and reproduction also include stochastic elements. A random $u[0,1]$ number is compared to a fixed probability to determine mortality, nest predation and successful hatching. The father of each egg is selected randomly with replacement from the sperm storage of the mother, and the natal site for each clutch is chosen at random from the burrows of the mother's home range. The size of each clutch is chosen from a normal distribution estimated from the literature. When new tortoises are created, alleles from the mother and father are mixed stochastically according to Mendelian inheritance.

5. INITIALIZATION

The simulation is initialized with active and inactive adult burrows from a burrow survey of FB. We chose to initialize the simulation with active and inactive adult burrows because those burrows could reasonably be expected to be occupied by adults (Stober and Smith 2010, Berish et al. 2012); this is appropriate because only adults occupy burrows in the simulation. The size of the initial tortoise population is estimated by multiplying the number of detected burrows by a conversion factor (Nomani et al. 2008, Stober and Smith 2010) that accounts for burrow occupancy. We used a conversion factor of 0.327 adult, subadult and juvenile tortoises per active or inactive adult burrow, an occupancy rate that was estimated directly from a recent intensive burrow survey of a portion of FB (Staff of Fort Benning Conservation Branch 2012). In this survey, burrow size (indicating the lifestage of the occupying tortoise, Alford 1980) and activity were recorded in the field, and occupancy at each burrow was established with a burrow camera (Nomani et al. 2008).

To populate the landscape with tortoises initially, we assume a stable age distribution at the beginning of each Monte Carlo iteration. Hatchlings are expected to comprise a large proportion of gopher tortoise populations, but are not usually encountered in surveys (Pike 2006). Therefore, we used life-stage-specific growth, mortality and fecundity rates estimated from the literature (parameters and sources listed in Table C6) and the matrix population methods of Caswell (2001) in the popbio package for R (Stubben et al. 2013) to estimate the stable stage distribution and the age-within-stage distribution that is characteristic of a population given the estimated demographic parameters. The initial population size estimated from the stable lifestage distribution and number of initial burrows on the landscape for each simulation approach is given in Table C4. Initial home ranges for adult tortoises are assigned by choosing a start burrow at random from initial burrows (see Assign home range submodels, Section 7); immature tortoises are initialized on the landscape at a current location chosen at random from initial burrow locations.

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Table C4. Initial population size for each simulation landscape. Tortoise population size was estimated by multiplying the number of initial burrows by a conversion factor determined empirically. The conversion factor was modified to account for the expected proportion of hatchlings in the population.

Lifestage	Simulation landscape			
	shortPOM ¹	LEA ²	ACUB ³	Pre-settlement ⁴ (longPOM)
Adults	1,259	1,287	108	58,977
Subadults	602	615	52	32,168
Juveniles	288	294	25	16,106
Hatchlings	1,015	1,038	87	57,421
Total	3,163	3,234	271	164,673

¹ Estimated population size based on 1999 USFWS survey and application of simulated annealing (i.e., 5B.

Burrow Pattern Prediction), which uses the 1999 USFWS survey as a template to predict burrow locations in the NE impact area.

² Estimated population size based on 2008-2010 JCA survey and application of simulated annealing (i.e., 5B.

Burrow Pattern Prediction), which uses the 2008-2010 JCA survey as a template to predict burrow locations in unsurveyed areas, including the NE impact area.

³ Estimated population size on ACUB properties based on surveyed burrows on three properties owned by The Nature Conservancy (Brown Springs, Almo, and Blackjack).

⁴ Estimated population size based on application of simulated annealing (5B. Burrow Pattern Prediction), which uses the 1999 USFWS survey, 2008-2010 JCA survey, and C. Guyer burrow surveys in high quality habitat as a template to predict burrows in our estimated pre-settlement habitat.

5A. INITIALIZING GENETICS

Each founder tortoise was initialized with 32 diploid neutral genetic loci. The first locus assumed that every founding individual is heterozygous and contains two unique alleles (i.e., total alleles = 2 x number of individuals in the founding population, an Infinite Alleles Model (IAM) of genetic variation).

For LEA and shortPOM, the remaining 31 loci were initialized using allele frequencies corresponding to those observed in the 31 neutral microsatellite loci from the 100 genetic field samples taken in 2009 (Kreiser et al. 2013). For each founder microsatellite locus, the probability of choosing an allele was proportional to its observed frequency at the corresponding microsatellite locus. Importantly, the same random process was used to assign alleles to founders regardless of their spatial location. Therefore, any spatial-genetic structure initially present in the founder population reflects this random process.

For longPOM, which is run over 683 years to provide sufficient time for model rules to possibly generate spatial

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genetic structure, we set the total number of all unique alleles present at all microsatellite loci to correspond to 116% of that observed in the field sample (from 200 increased to 232 unique alleles). We did this so that at the end of 683 years, the total number of unique alleles at microsatellite loci present in a sample of 100 individuals would be approximately equal to that observed in the field sample (200). To increase the number of unique alleles, we duplicated the observed frequencies of 32 randomly chosen alleles.

5B. BURROW PATTERN PREDICTION

Because the simulated tortoise population is initialized at a size proportional to the number of initial burrows on the landscape, it is important to account for burrows that may have occurred in unsurveyed areas. The objective of burrow pattern prediction for the shortPOM simulation was to estimate the number and spatial associations of burrows in the NE impact area (Figure C1). In contrast, the object of LEA burrow pattern prediction was to predict burrow locations in areas not included in the John Carter and Associates (JCA) survey, which also includes the NE impact area. For the pre-settlement landscape, which provides initial conditions for longPOM, burrows were predicted across the Chattahoochee Fall Line, including areas outside of FB to reflect population status prior to European settlement. This section begins by describing the approach for LEA and shortPOM, which are very similar, and then burrow prediction for the pre-settlement landscape is described.

We used point pattern analysis and the habitat suitability model corresponding to each simulation approach to estimate a realistic configuration of burrows at realistic densities expected at a given habitat quality. To analyze burrow point patterns and reconstruct burrow patterns we used Programita (v. 2012; Wiegand et al. 2013), a software package that characterizes point patterns using multiple statistics. These statistics include $g(k)$, the pair correlation function, which is the mean expected density of points in a ring with radius r and width of radius Δr ; $D_k(r)$, the cumulative nearest neighbor distribution, which is the proportion of points where the k^{th} nearest neighbor is distance r away; $H_s(r)$, the spherical contact distribution, which is the proportion of test locations (not in the pattern) where the nearest neighbor is less than distance r away; and $nn(k)$, the nearest neighbor count, which is the mean distance to the k^{th} nearest neighbor.

Programita uses simulated annealing to reconstruct a point pattern with spatial characteristics that are similar to that of a template pattern. Simulated annealing begins by first generating a random pattern containing the same number of points as the template pattern. The spatial association of points in this random pattern is compared to the template using the four statistics described above. Then a random point in the pattern is moved to a new location. If the new location increases the similarity of the pattern to the template it is accepted; otherwise it is moved back to its original location. This process is repeated until the pattern crosses a similarity threshold empirically determined by the authors of Programita, or after 40,000 iterations are completed.

We began burrow reconstructions by predicting the appropriate density of burrows for a given habitat quality

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using Ordinary Least Squares (OLS) regression. Best professional judgment suggested that a grain of 2100 m would be useful for characterizing the number of burrows across a variety of habitat densities. We used results from the JCA burrow survey, along with predictions from our global habitat model (the model providing the strongest prediction of burrow density), to obtain the following regression equation:

$$\text{Number of Burrows} = 0.0875 * \sum (\text{Habitat Scores}) + 2.60$$

Equation 1: OLS regression equation relating habitat scores to the number of burrows for 2100 X 2100 m areas. Adjusted $R^2 = 0.734$.

Because the NE impact area is not included in soil surveys, we were unable to estimate habitat quality directly. Instead, we estimated habitat quality inside the impact area by averaging habitat quality scores estimated by the abiotic model in areas bordering the impact area. We used the abiotic habitat model rather than the global habitat model because the latter incorporates vegetative characteristics that likely did not exist in 1999, the year that the POM simulation is initialized (Table C1). We found the average habitat quality on the border was 0.3345. We assumed homogeneous habitat quality across the impact area and substituted this value into Eq. 1 to estimate the number of burrows occurring in the impact area.

To predict burrow patterns over the NE impact area, we then identified template burrow patterns (2100 m grid cells) from the U.S. Fish and Wildlife Service (USFWS) burrow survey with the same density of burrows as was predicted by Eq. 1 to occur in the impact area. These templates were selected at random with replacement and loaded into Programita. Programita then used simulated annealing, as described above, to reconstruct the burrow pattern observed in a selected template in each 2100 m grid cell of the NE impact area. When a suitable predicted burrow pattern was found, the predicted burrow patterns were then placed into the NE impact area.

For the LEA landscape, burrows were predicted in the NE impact area and in areas that were unsurveyed by JCA. We used the same process as was used for the POM landscape, except that template patterns were chosen from the JCA burrow survey and the global habitat model was used. The selection of templates for the LEA landscape also included a larger diversity of 2100 m grid cells with different burrow densities, reflecting the distribution of estimated habitat quality across unsurveyed areas.

To predict burrow patterns for the pre-settlement (baseline) landscape, we had to estimate burrow densities to reflect historic population structure across the Chattahoochee Fall Line prior to European settlement. To approximate the expected high densities that were present on the ancestral FB landscape, we drew from burrow surveys recorded by Dr. C. Guyer at six sites across the species' range. These sites included gopher tortoise populations in Mobile County Alabama, Camp Shelby in Mississippi, Conecuh National Forest (site #4) in Alabama, Wade Tract in Thompson County Georgia, Green Grove at Jones Ecological Research Center in

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Georgia, and Solon Dixon Forestry Education Center in Alabama (Guyer et al. 2012). Because the spatial extent of the Guyer study areas was smaller than the 2100 m grid size used in pattern reconstruction, we replicated the burrow surveys and combined them to achieve a minimum of 6300 m grid (therefore providing nine replicates of 2100 m grid cells). We used block resampling, using the spatstat library in R, to obscure replication artifacts that change point pattern associations due to replicating grids (Baddeley and Turner 2005). The nine resampled replicates were then available for selection as template patterns in Programita.

As described under landscape above, we constructed a habitat suitability model for the pre-settlement landscape by first estimating abiotic habitat suitability. This pre-settlement habitat suitability model incorporated only topography, soil, and distance to waterbodies (i.e., those aspects of the global model that are not expected to have been affected by human activities, Table C1). We then estimated an upper limit for burrow density using burrow surveys at two of Dr. C. Guyer's sites where regular burns have maintained high-quality habitat thought to be typical of the ancestral longleaf pine ecosystem (Van Lear et al. 2005). These two sites, the Jones Ecological Research Center located in Baker County, Georgia and the Wade Tract, a private property in Thomas County, Georgia, host large gopher tortoise populations and are recognized as the best remaining habitat in the northern portion of the species' range (Johnson et al. 2007, Guyer et al. 2012).

We first assumed that the burrow template from these two high-quality sites with the greatest density of burrows had uniform habitat quality of one (i.e., maximum possible habitat quality score). The number of burrows in this template was used as the dependent variable in Eq. 1; this allowed us to solve for the slope algebraically to derive Eq. 2.

$$\text{Number of Burrows} = 0.3062 * \sum (\text{Habitat Scores}) + 2.60$$

Equation 2: Adjusted OLS regression equation relating habitat scores to the theoretical number of burrows for 2100 X 2100 m areas prior to European settlement.

We used Eq. 2 to estimate the appropriate density of burrows for the pre-settlement grid cells. Because habitat values across the pre-settlement map varied more greatly than observed on C. Guyer's high density sites, we also randomly selected templates for reconstruction from the USFWS burrow survey and the JCA burrow survey in addition to the block-resampled templates that were created from the Guyer burrow surveys. These templates were then used to estimate summary statistics describing spatial associations of burrows. Simulated annealing was performed in Programita to reconstruct template point patterns, and finally, reconstructed burrow patterns were reassembled into the pre-settlement burrow pattern.

5C. POM APPROACH

The burrow survey used to initialize the shortPOM simulation experiment was conducted in 1999 by the USFWS

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(the USFWS survey). The survey was complete over the installation, except for impact areas in the interior of the installation, which contain unexploded artillery and were not surveyed (Figure C1). While the southwestern impact area is of low quality habitat, the NE impact area is assumed to have higher quality habitat and a substantial number of tortoises (Mark Thornton, Ft. Benning, personal communication). Therefore, burrow locations for the NE impact area were estimated as described under burrow pattern prediction above. The initial distribution of burrows on the shortPOM landscape is shown in Figure C2.

The longPOM experiment was initialized with the pre-settlement landscape including predicted burrow locations (Figure C3). Burrow locations were estimated following the burrow reconstruction process outlined above.

5D. LEA APPROACH

The burrow survey of FB used to initialize the LEA simulation experiment was conducted in the summers of 2008 – 2010 by JCA (the JCA survey). Time constraints restricted the survey to areas of medium- to high-quality habitat, leaving substantial portions of the installation in addition to the impact areas unsurveyed (Figure C4). Therefore burrow locations were estimated in unsurveyed areas across FB, including the NE impact area, as described under burrow pattern prediction above.

In addition to surveyed and predicted burrow locations on FB, for the LEA simulation we included active and inactive adult burrows from recent burrow surveys on two ACUB properties owned by The Nature Conservancy. The Brown Springs property adjacent to FB was surveyed in 2010 by Conservation Crew staff at FB (Travis Thornley, FB Conservation Crew staff, personal communication), while burrows on the Almo and Blackjack Crossing properties were surveyed in 2010 by staff of the Joseph W. Jones Ecological Research Center (Michele Elmore, TNC, personal communication). Although the Almo and Blackjack Crossing surveys were line transect distance sampling surveys and not complete over the two properties (Michele Elmore, TNC, personal communication), we validated their use by comparing the Almo survey to a complete survey of the same area in 2006 (Hermann and Sorrell 2006). While the 2006 survey reported 236 burrows, the 2010 survey included 234. Therefore we feel it is appropriate to include the more recent surveys.

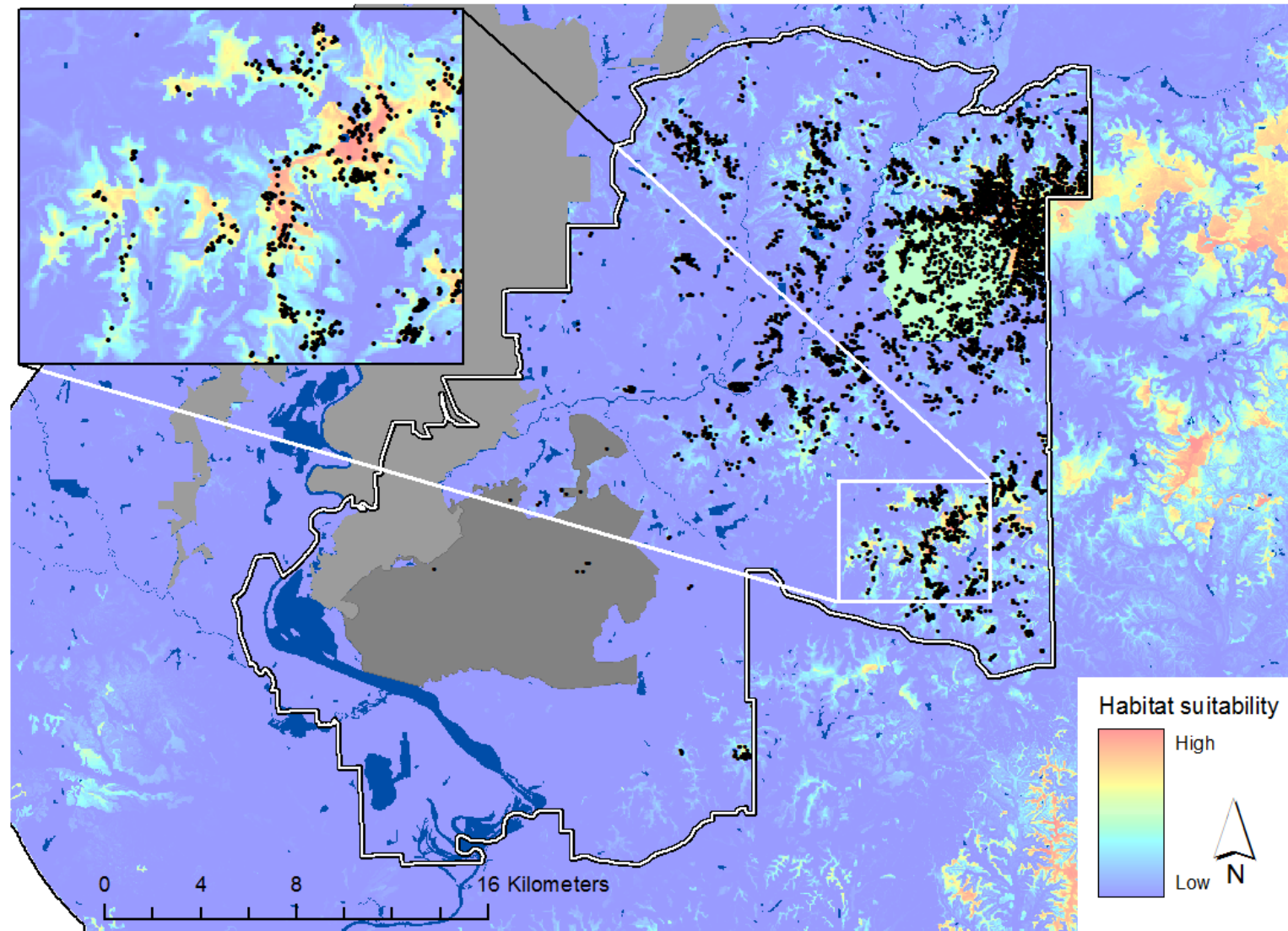


Figure C2. Initial conditions for the shortPOM simulation landscape. Burrow locations (black points) comprise the 1999 USFWS survey of Ft. Benning and predicted locations in the NE impact area, where burrow locations were estimated following the process outlined in burrow pattern prediction. Habitat suitability values were calculated with the abiotic resource selection probability function (Table C2; see Landscape, Section 2).

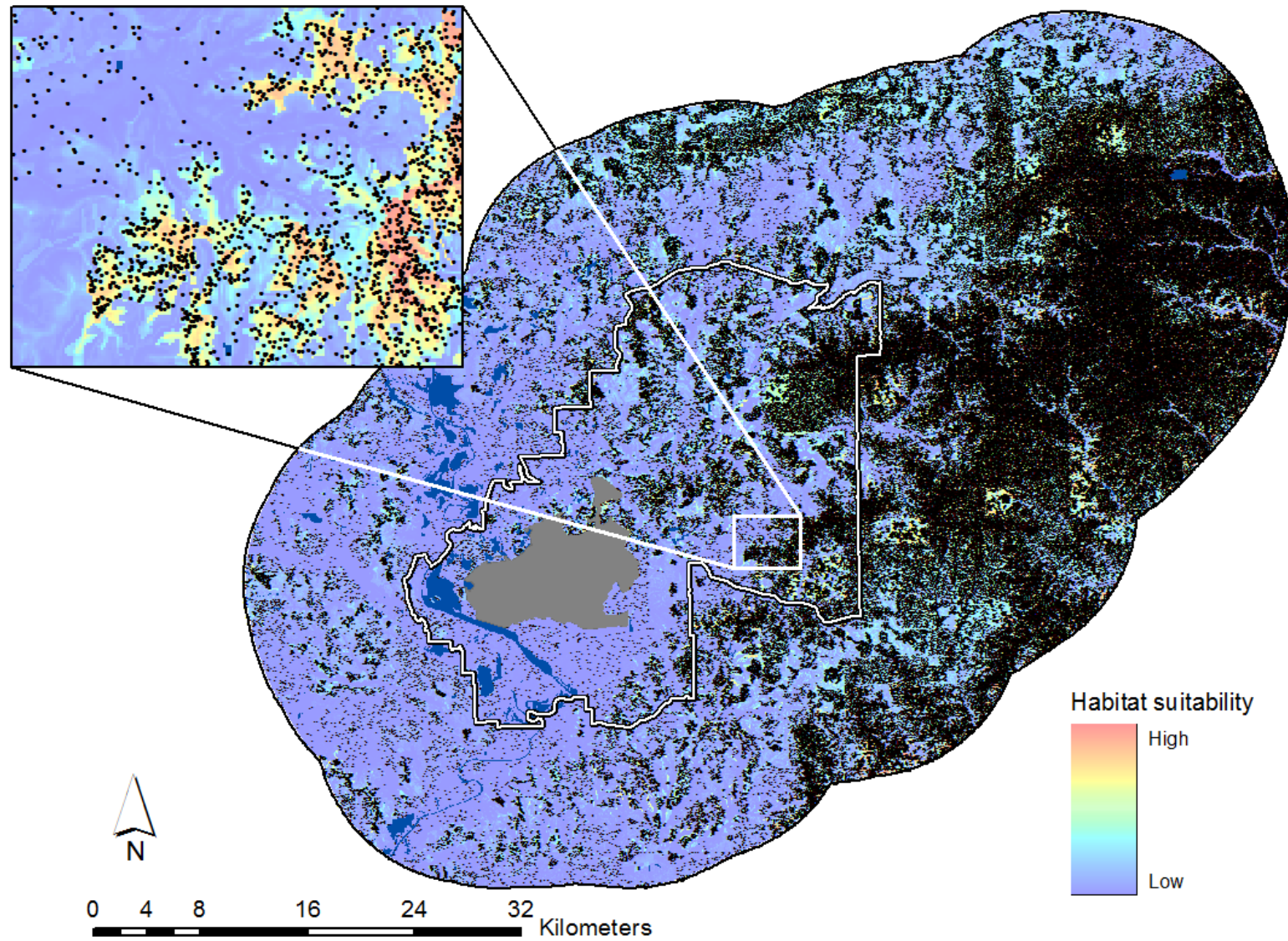


Figure C3. Initial conditions for the longPOM simulation experiment, showing the pre-settlement landscape and estimated locations of pre-settlement burrows (black points). Burrow locations were estimated as described under burrow pattern prediction. Habitat suitability values were calculated with the pre-settlement resource selection probability function (Table C2; see Landscape, Section 2).

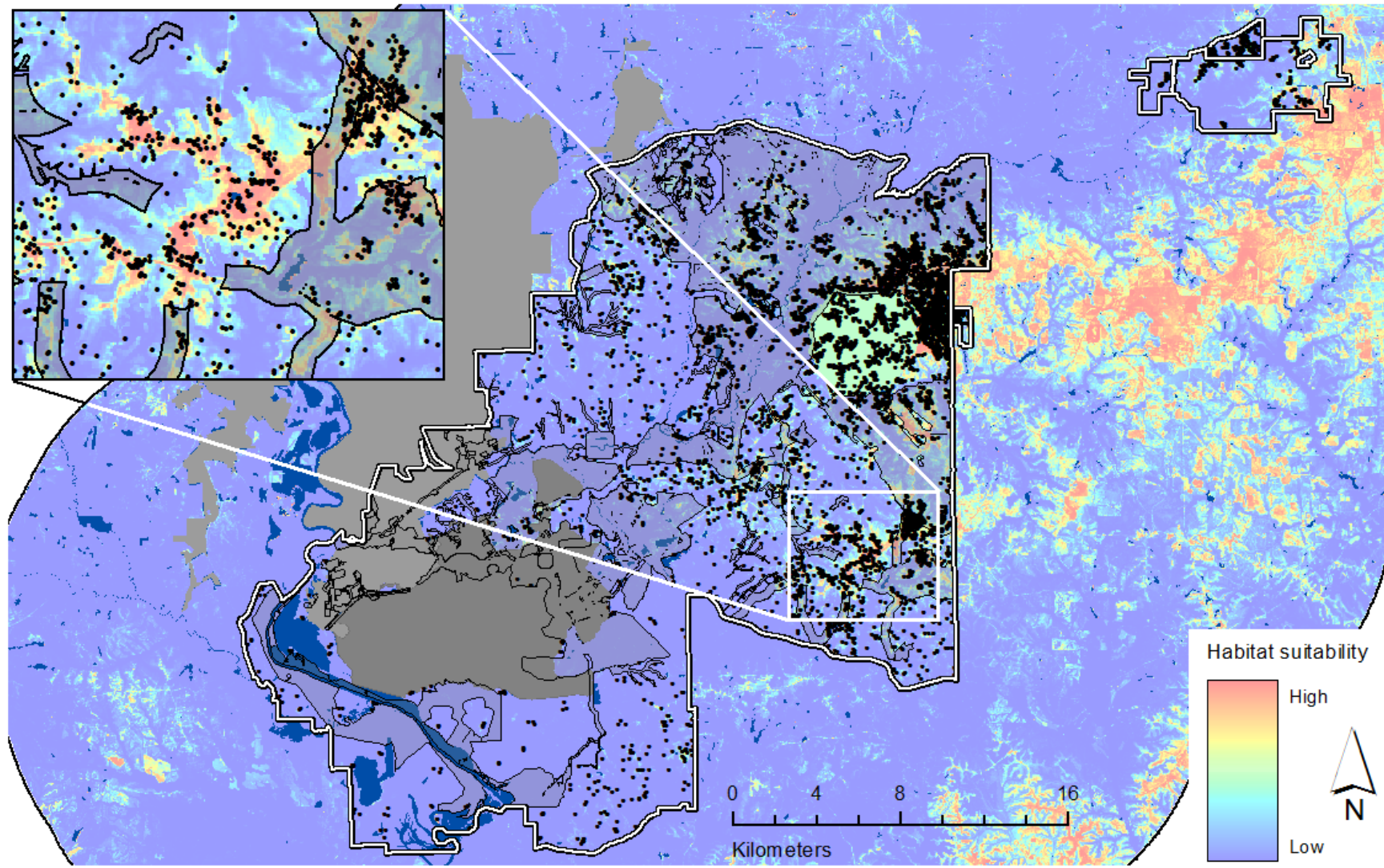


Figure C4. Initial conditions for the LEA simulation experiment, including burrow locations (black points) from the JCA survey of FB and from burrow surveys on three ACUB properties owned by The Nature Conservancy. Areas on FB that were surveyed by JCA are outlined in black; burrow locations in unsurveyed areas on FB including the NE impact area were estimated with burrow pattern prediction. Habitat suitability values were calculated with the global resource selection probability function (Table C2; see Landscape, Section 2).

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Landscape Treatments

To contrast gopher tortoise population viability across different land use scenarios, multiple landscape treatments were developed for the LEA simulation. Landscape treatments consist of removal of GT habitat, for example due to construction, and relocation of gopher tortoises displaced by such impacts. Potential relocation properties were identified from ACUB parcels currently owned by The Nature Conservancy (TNC). Relocation areas were categorized based on TNC management unit (Figure C5).

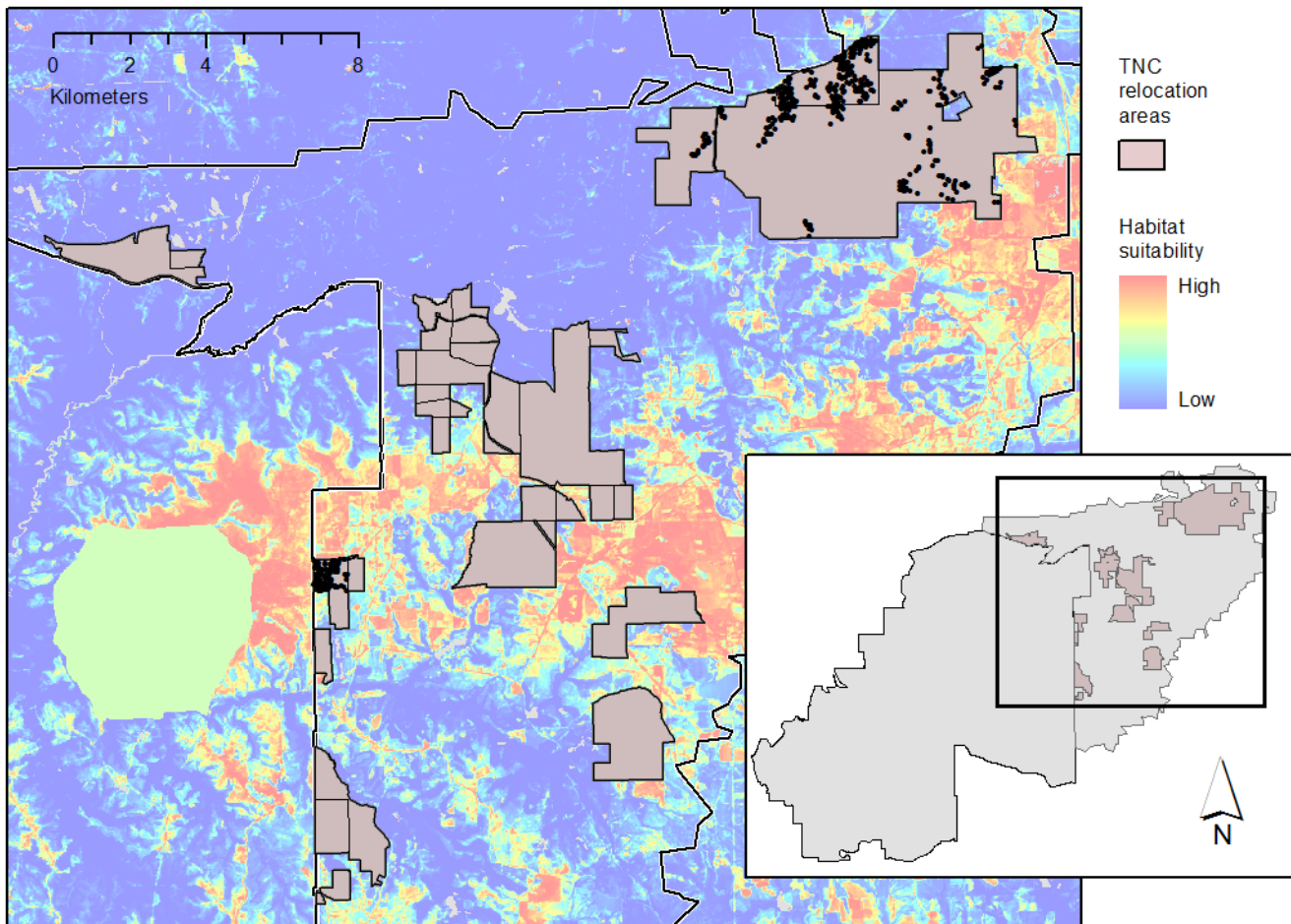


Figure C5. Relocation areas on ACUB owned by The Nature Conservancy. Each potential relocation area (large shaded polygon) was formed by dissolving adjacent properties, outlined in black, within TNC management units. Black dots show burrow locations on TNC properties from burrow surveys completed in 2010. Habitat suitability values shown are those for the LEA landscape, using the global resource selection probability function. Inset map shows location of relocation areas on ACUB.

We used the detailed guidelines of the Florida Fish and Wildlife Conservation Commission (FWC; Florida Fish and Wildlife Conservation Commission 2008) to structure both removal and relocation landscape treatments. When tortoises were removed from removal areas, we simulated perfect detection and capture of all lifestages. Adults occupying any burrow inside the removal area and immature tortoises with a current location inside the

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removal area were removed. When pens were used to acclimate tortoises at relocation areas, all lifestages (including hatchlings) were also assumed to be perfectly enclosed. Following removal, habitat value scores in the removal area were changed to zero, and tortoises were not allowed to establish burrows in that area. When emigrating tortoises encountered the removal area following the removal event, the area was assumed to have habitat suitability of zero (see Emigration submodel, Section 7).

The FWC guidelines use stepped evaluation criteria to determine maximum stocking density of recipient sites from site factors such as soil type, vegetation density and legal status of the property (Florida Fish and Wildlife Conservation Commission 2008). Sites with deep sandy soils, low canopy density, and designated protection for conservation are allowed to host a greater density of tortoises. The maximum allowable density of tortoises varies from two (in acceptable habitat) to four (in desirable habitat) adult and subadult tortoises per acre (or five to ten adult and subadult tortoises per ha), based on these characteristics. Because the global habitat model applied to the LEA landscape incorporates soil and vegetation characteristics similar to those that are included in the FWC criteria (Table C1), we adapted the FWC approach by calculating the stocking density of each potential relocation property from the distribution of habitat suitability scores inside the property. Values for acceptable and desirable habitat were defined using the relationship between burrow occurrence and habitat quality observed on FB in the 2008 – 2010 time frame. We used the distribution of habitat scores for 30 m grid cells where active or inactive burrows were located in the JCA survey (Figure C6).

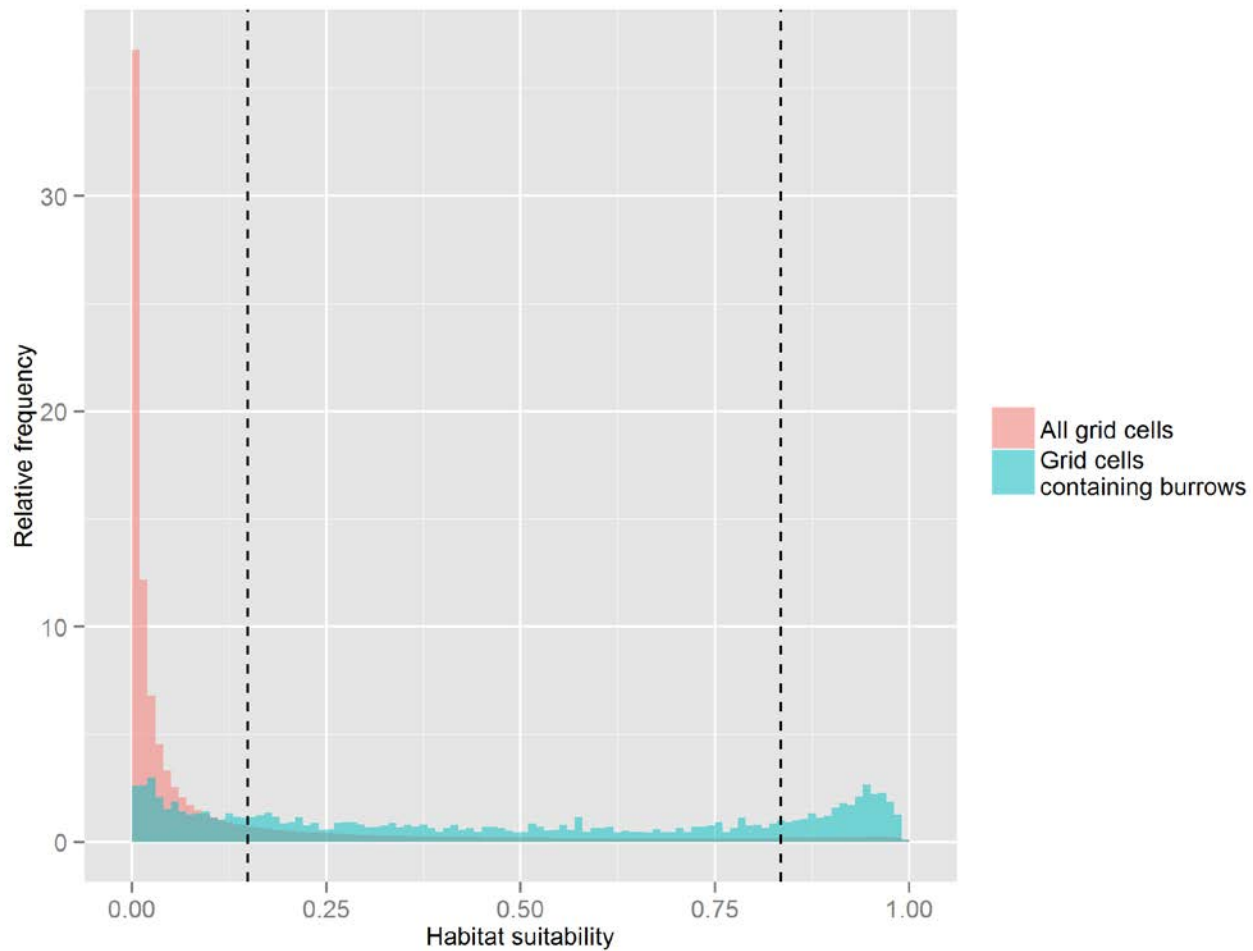


Figure C6. Distribution of habitat suitability values in grid cells containing at least one active or inactive burrow from the JCA survey (blue) and in all grid cells (pink), where habitat suitability is defined with the global model. Frequency values for each distribution were normalized so that relative frequencies within the distribution sum to one, facilitating comparison of the two distributions. Habitat suitability values that were used to define acceptable and desirable habitat in recipient sites are designated with dashed lines.

Acceptable habitat quality was defined as habitat values above the 25th percentile of the distribution of habitat scores in grid cells containing surveyed burrows (0.149), so that areas at or above this value were assigned the lower stocking density of five tortoises per ha. Desirable habitat quality was defined as above the 75th percentile of the distribution (0.835), so these areas were assigned the upper stocking density of ten tortoises per ha. The capacity of each TNC property, in terms of subadult and adult tortoises, was calculated by summing the area in the property above these two values (e.g., Figure C7).

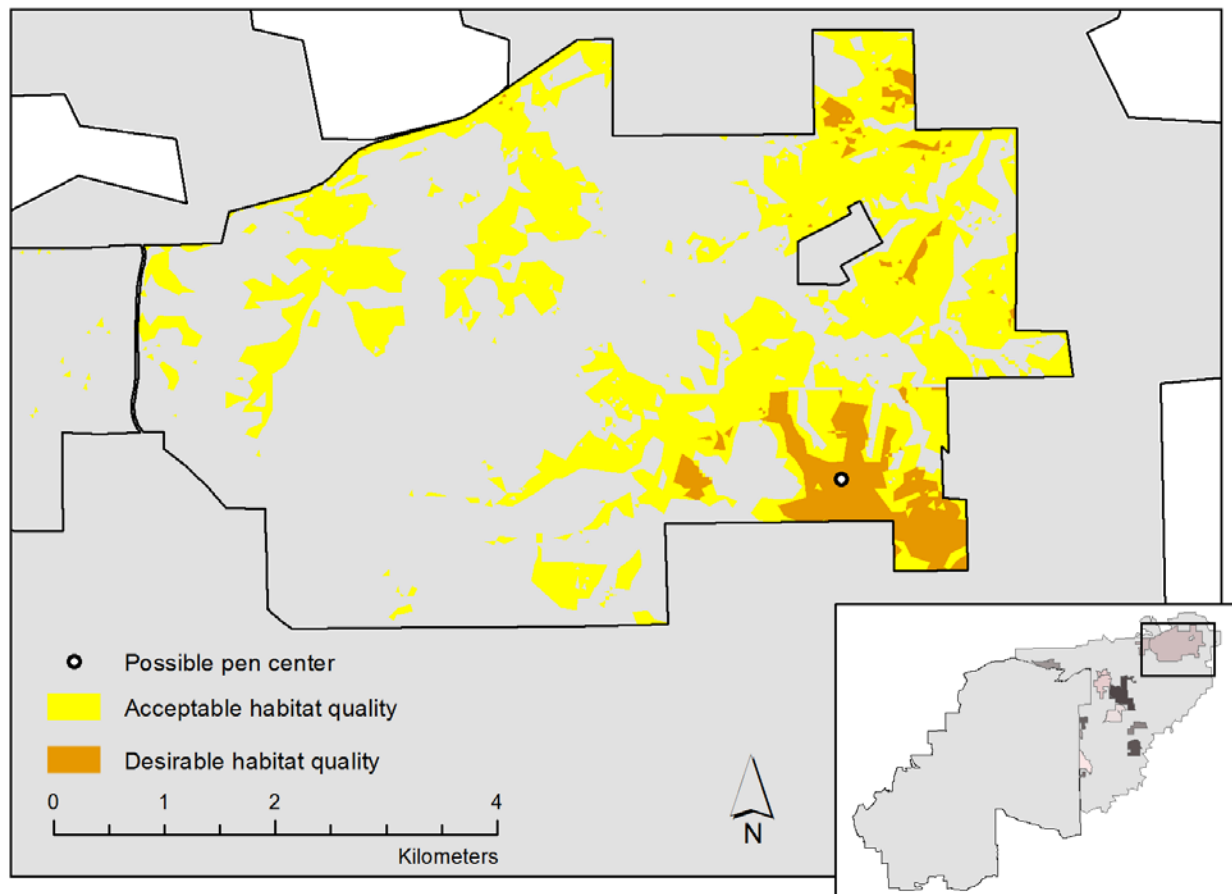


Figure C7. Distribution of acceptable and desirable habitat inside Blackjack Crossing, an example TNC relocation area. Adult and subadult capacity for each relocation area was calculated from the area of acceptable and desirable habitat for the property, where acceptable and desirable habitat were identified from threshold habitat suitability values. For this property, capacity according to habitat quality was calculated to be 6,115 subadult and adult tortoises. Static pen centers were located in high quality habitat.

When tortoises were relocated, they were placed in acclimation pens for one year as is recommended by FWC guidelines (Florida Fish and Wildlife Conservation Commission 2008). We placed static pen centers in each relocation property in areas of high quality habitat (Figure C7), and determined the size of the pen dynamically in the simulation to accommodate the number of subadult and adult tortoises to be relocated to the property. When the base stocking density is calculated from the amount of acceptable and desirable habitat inside the pen (i.e., using the same method as is done for the recipient site as a whole), FWC guidelines require that maximum tortoise density inside pens should be 1.5 times the base stocking density of the pen. We conservatively assumed that pens would consist of acceptable habitat only, and therefore assigned all pens a stocking density of 7.5 adult and subadult tortoises per ha of the pen (i.e., 1.5×5 adult and subadult tortoises per ha (the allowable stocking density in acceptable habitat)).

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Because little is known about how home ranges are established in pens following relocation, relocated tortoises were assigned home ranges of one to three burrows to accommodate the high density of tortoises in pens. The first burrow of the home range was located in a random grid cell within the pen with habitat suitability greater than or equal to 0.551 (the median habitat suitability of grid cells containing active or inactive surveyed burrows; Figure C6). If an existing burrow was already available within a radius of five cells from the random starting cell, the tortoise occupied it and dug 1 – 2 additional burrows (number of burrows chosen randomly). If no existing burrow could be located, the tortoise was assigned to dig 1 – 3 burrows, again with the number of burrows chosen randomly. When digging burrows, tortoises were restricted to dig them in areas above a threshold habitat quality (again, the median habitat suitability of grid cells containing active or inactive surveyed burrows, 0.551) and within a range of distances from existing burrows (see details under Dig burrows submodel, Section 7), but otherwise without regard to locations of other tortoises. Immature tortoises were assigned a random location within the pen in a grid cell with habitat suitability over 0.551. Tortoises were not allowed to emigrate in the first year following relocation, but after that year they received home ranges and emigrated as all other tortoises in the simulation (without regard to any boundaries).

We included **recent relocation** events that took place on FB in 2009 and 2010 with all management scenarios to include the effects of management actions that have already been taken. While other relocations have been performed on FB, these were the only events for which we could obtain detailed location data for both removal and relocation areas. During these relocation events, tortoises were moved from areas of the installation where construction was expected to cause habitat destruction. All burrows in the impacted area were trapped, and recovered tortoises were relocated to selected areas of high quality habitat on the installation (Gregory Brooks, FB Conservation Crew, personal communication). Staff at FB provided us with shapefiles of trapped burrow locations and relocation areas (Figure C8).

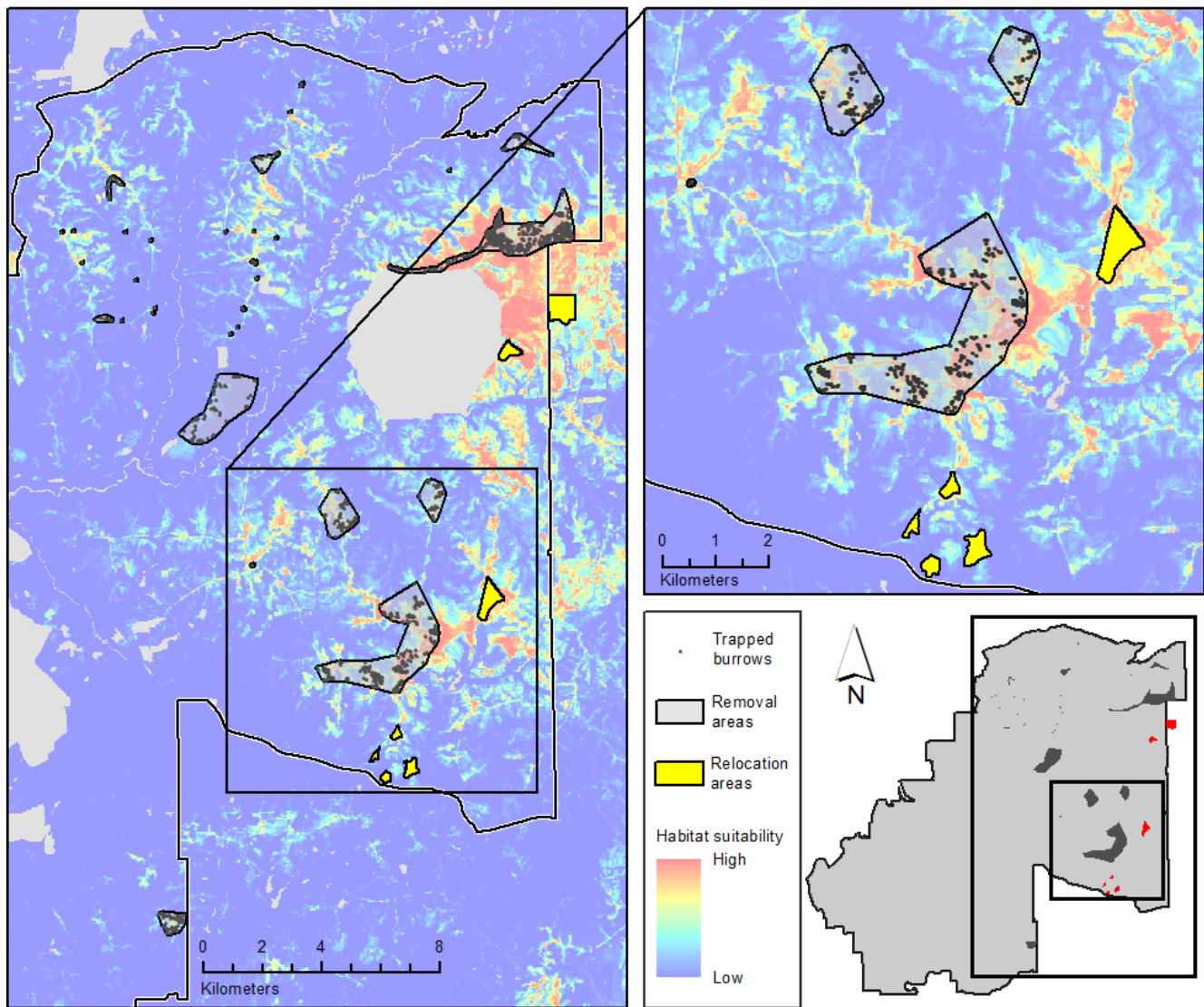


Figure C8. Removal and relocation areas included in recent relocations. Removal areas (transparent grey polygons) were placed over the locations of burrows that were trapped in 2009 and 2010 (dark grey points). Where trapped burrow clusters could not easily be identified by eye, burrow locations were buffered by 60 m. Lower inset shows the locations of removal and relocation areas on Ft. Benning.

Because the available data on removal areas depicted burrow locations only, it was necessary to first interpolate the areas impacted by construction activities that would be treated as removal areas in the simulation (i.e., create polygon removal areas from burrow location points). We created polygon removal areas by first buffering trapped burrow locations by 60 m. When clusters of burrows could easily be visually identified, we drew bounding polygons around those clusters. Burrows that could not easily be identified in clusters were bounded by the 60 m buffer only (Figure C8).

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During simulated recent relocations, tortoises are removed from the removal areas as described previously (i.e., assuming perfect detection of adults occupying any burrows within the removal area and all immature tortoises with current location inside the removal area). Because we were unsure whether the historical relocation areas shared with us by Benning staff represented pens, we did not use pens for the recent relocations but chose instead to “release” tortoises at random locations within relocation areas at grid cells with habitat suitability values above 0.551. Because the exact number of tortoises removed in the simulation could differ from the number of tortoises relocated in reality (due to stochastic processes included), we subdivided the relocated tortoises across the four recent relocation areas based on the percent of tortoises moved there by FB crews.

6. INPUT DATA / OBSERVED PATTERNS

6A. POM APPROACH: SUMMARY STATISTICS

Summary statistics are observable components of population structure affected by life history traits thought to underlie population persistence (Martinez et al. 2011). For example, simulating realistic home range characteristics is crucial for modeling reproduction and gene flow, because the simulated sperm storage of each adult female is populated by males with whom she overlaps (see Assign home range and Reproduction submodels, Section 7). Because data describing home ranges were not available from FB, observed patterns describing home range size and home range overlap were drawn from an unpublished multi-year, multi-site radio telemetry database (C. Guyer unpublished data from Mobile Co. AL, Camp Shelby, and Conecuh National Forest site #4). Detailed site descriptions can be found in Guyer et al. (2012). We used the Guyer telemetry database to characterize home ranges of 32 male and 30 female tortoises that had been located at least 50 times over 11 – 12 months, providing sufficient sampling to describe the burrows occupied in one year (Eubanks et al. 2003). For males and females separately, we constructed cumulative distributions for two important home range characteristics: the number of burrows in the home range, and the percent of burrows in each individual’s home range that were also occupied by a member of the opposite sex (i.e., percent home range overlap). We chose to summarize the data as cumulative distributions as they do not fit expectations of traditional distributions such as Gaussian or Poisson. The bin width for the number of burrows in the home range was 1, and for percent overlap with the opposite sex the bin width was 0.1, or 10%.

To compare these observed patterns with tortoise home ranges in the last year of the POM simulation, we construct cumulative distributions for the two home range metrics for all adults in the simulated population using bin widths identical to those used for observed distributions (Figure C9). The ability of each model parameterization to approximate similar home range patterns observed in the field is then estimated using sums of squares (SSq^{HR}):

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$$SSq^{HR} = \sum_{n=1}^B (O_n - S_n)^2$$

Where B is the number of bins used to describe the cumulative distribution, O is the cumulative probability of the number of burrows or overlap with the opposite sex observed in home ranges in the field, and S is the cumulative probability of the number of burrows or overlap with the opposite sex generated by the simulation. The average values of SSq^{HR} for number of burrows in the home range and home range overlap for each sex were calculated for each parameterization across Monte Carlo iterations to control for stochasticity in the simulation.

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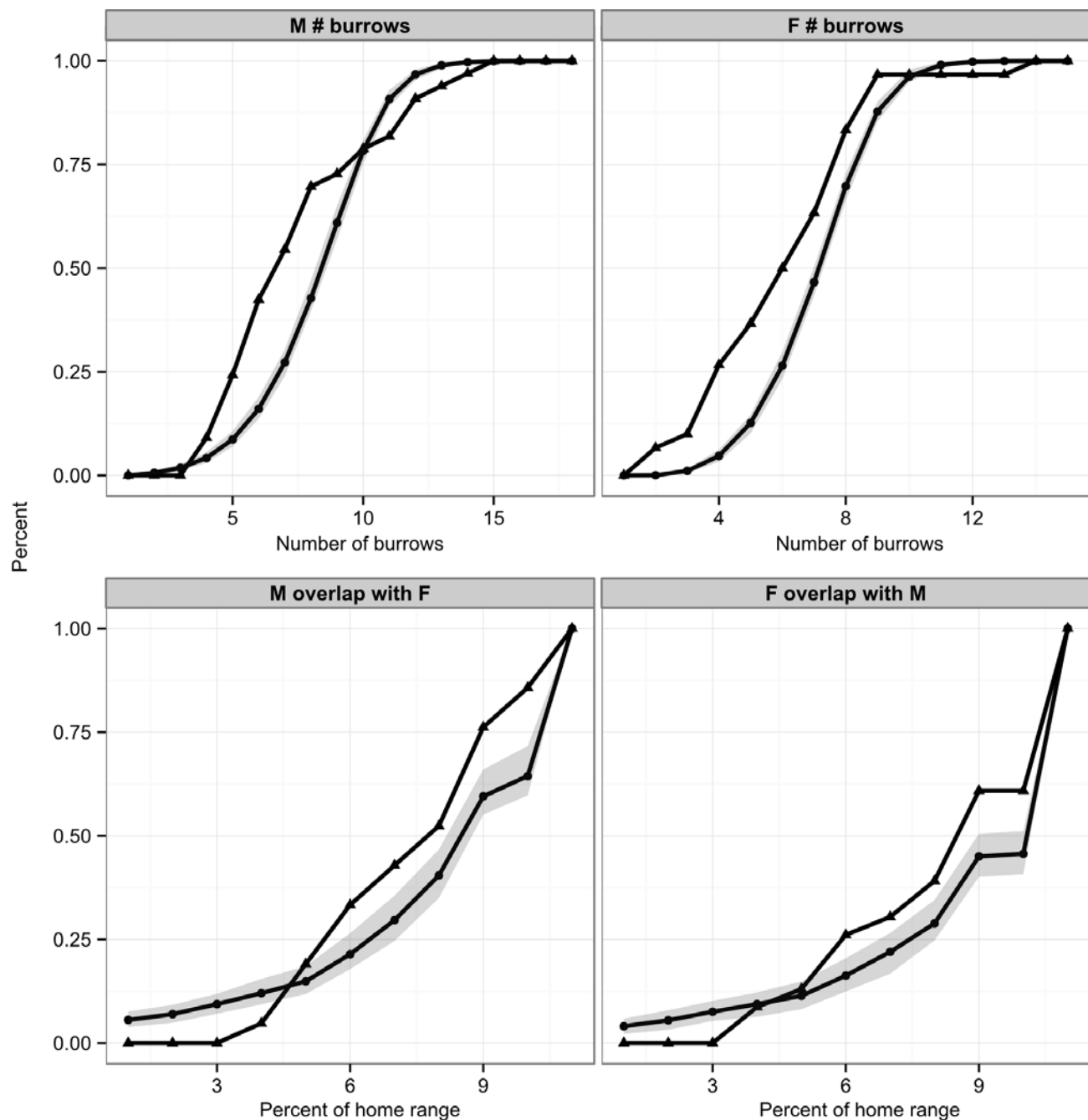


Figure C9. Cumulative distribution of number of burrows in a male's home range, number of burrows in a female's home range, percent of male home range **overlapping** with females, and percent of female home range overlapping with males. Observed data taken from C. Guyer unpublished data from Mobile Co. AL, Camp Shelby, Conecuh National Forest site #4; diamonds. Simulated data taken from year 2009 of the 683 year longPOM experiment; circles, shading represent the 95th percentile of results from the simulation.

Another useful summary statistic is the univariate O-ring describing adult burrow patterns (O_r^{aa}). The O_r^{aa} statistic measures the spatial autocorrelation, or spatial dependency, of adult burrows across the landscape. High

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burrow density is important for the maintenance of gopher tortoise social interactions (Guyer et al. 2012), and burrow surveys are the most common data available to describe gopher tortoise populations. However, a single value for density, determined over an entire study area, does not capture much of the spatial information contained in a complex pattern such as a burrow survey (Wiegand and Moloney 2004). O_r^{aa} is a measure of the average density of points in a point pattern (e.g., a burrow survey) contained in ring-shaped regions over a variety of spatial scales, which allows us to characterize the spatial autocorrelation of burrows in a more informative manner.

Here we focus only on adult burrows because they have the highest reproductive value (Boglioli et al. 2003) and our simulation does not currently characterize home range use of immature tortoises due to a lack of research in this area. O_r^{aa} is calculated by constructing a series of rings at different lag distances centered on each point: in our case the point is a burrow. All of the rings have the same width, in our case 120 m. We chose 120 m as this represents an average diameter of male home ranges (around 1.26 ha; McRae et al. 1981, Smith et al. 1997, Eubanks et al. 2003, Yager et al. 2007), thus providing a ring width big enough to capture individual home ranges but also small enough to characterize the change in spatial autocorrelation at multiple scales.

Rings with a width of 120 m were calculated at lag distances ranging from 120 – 6000 m. The number of points intersected by the ring was divided by the area of the ring. If part of the ring fell outside of the area that was surveyed for burrows (e.g., the boundary of FB or boundaries of the JCA burrow survey area), only the actual area surveyed was used as the area of the ring. The average value of this ratio was calculated for all rings at the same lag distance. This gives the O-ring statistic at lag distance r , or O_r^{aa} (Wiegand and Moloney 2004):

$$O_r^{aa} = \left(\sum_{p=1}^P \frac{\text{Points in } R(r,p)}{\text{Area of } R(r,p)} \right) / P$$

Where $R(r,p)$ is a ring at lag distance r and centered at the p^{th} point out of P points. O_r^{aa} was calculated across the areas sampled during the JCA burrow survey conducted in 2008-2010.

The same summary statistic was calculated within POM simulations in year 2009 using the burrow pattern generated by each parameterization. In order to control for differences in sample area, we restricted our analysis to simulated burrows in the area covered by the JCA survey. We compared the simulated values of O_r^{aa} to the empirical values calculated from the JCA survey (Figure C10). The comparison was formulated as a mean sum of squared errors where for each Monte Carlo iteration we calculated:

$$SSq^O = \sum_{r=1}^R (O_{r \text{ obs}}^{aa} - O_{r \text{ sim}}^{aa})^2$$

Where $O_{r \text{ obs}}^{aa}$ is the empirical value of the O-ring statistic at lag distance r , $O_{r \text{ sim}}^{aa}$ is the simulated value at

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lag distance r and R is the total number of lag distances tested (50). The average value of SSq^0 was calculated for each parameterization across Monte Carlo iterations to control for stochasticity in the simulation.

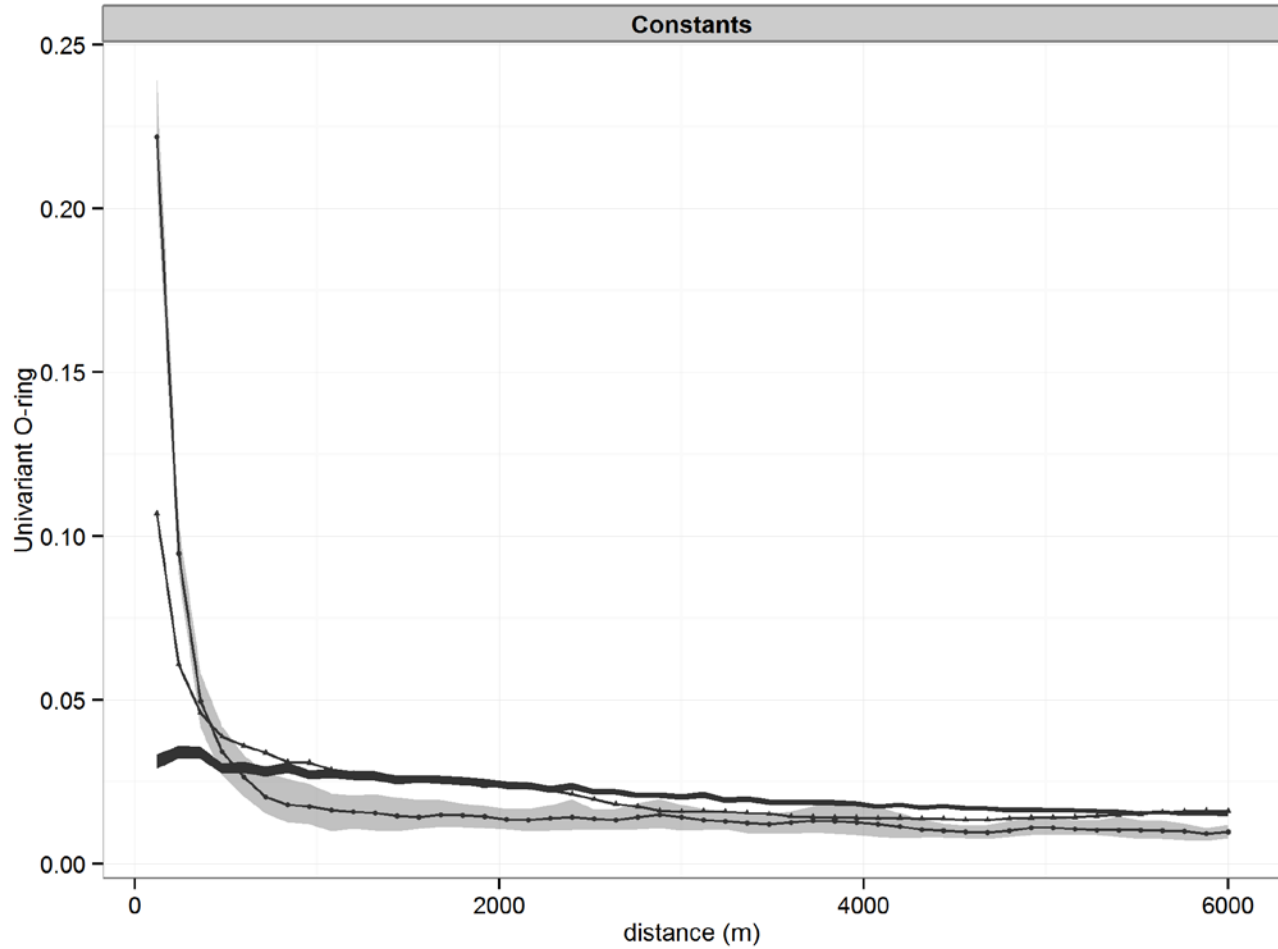


Figure C10. Comparison of univariate O-ring statistics (O_r^{aa}), representing the density of burrows within rings of 30 m width, observed in the J Carter survey (2008-2009), diamonds; estimated by a null model of observed data (i.e., non-homogeneous Poisson process), black envelope; estimated by the simulation, circles with the gray being 95th percentiles.

In order to quantify the correlation between gopher tortoise genetic diversity and habitat quality, we extended a ring index approach developed by Bruggeman et al. (2010). For this method we first calculated the total number of unique alleles per individual (TNA) from samples collected in the field. Then we calculated the O-ring statistic, $O_{r,p}^h$ to characterize the spatial autocorrelation of habitat at different lag distances from each of the field sample locations.

$$O_{r,p}^h = R(r,p)_{habitat} / R(r,p)_{area}$$

Where $R(r,p)$ is a ring-shaped window at lag distance r , centered at point p (i.e., the location of a genetically sampled gopher tortoise). $R(r,p)_{habitat}$ is the sum of the habitat model scores contained within the ring. $R(r,p)_{area}$

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is the area of the ring shaped window. If habitat model scores were only available for part of the window, then only that portion was included in the area (Wiegand and Moloney 2004). Like $O_{r,p}^{aa}$, $O_{r,p}^h$ was calculated for 50 non-overlapping ring sizes of 120 m width, from 120 m to 6000 m.

We used Spearman Rank Correlations to relate the TNA values with the $O_{r,p}^h$ values for each ring size r and sex s (resulting correlations will be symbolized as $\rho(r,s)_{obs}$). To determine if male and female genetic diversity differed in their correlation with habitat quality we performed the O-ring genetic correlations on each sex separately. The significance of correlations was determined using an asymptotic t-test with a 95% confidence level (Zar 1972). We applied this method to genetic data from 100 gopher tortoises (69 males and 31 females) sampled on FB in 2009 and genetically sequenced at 32 microsatellite loci (only 31 loci were included in subsequent analysis as the 32nd was not in *Hardy–Weinberg* equilibrium and therefore not a neutral genetic marker). Significant correlations were identified for females at distances at 240 m and 1560-3120 m (Figure C11). Significant distance classes were identified for males between 1560-1680 m (Figure C12).

Within the longPOM simulation, we replicated both the genetic sampling scheme conducted in 2009 on FB and the O-ring genetic correlation analysis. In order to replicate the 1 km x 1 km genetic sampling scheme applied in the field, we subdivided the simulation landscape using a regular 990 m x 990 m sampling grid, as we were constrained by the 30 m grain of our landscape. Individuals were then randomly selected from these areas without replacement (for both grid cells and individuals) until 100 individuals had been sampled. In order to eliminate the effect of sample size on the correlations when comparing simulated to empirical results, we further stipulated that exactly 69 males and 31 females (the sex ratio of the empirical genetic sample) should be sampled. If the maximum number of a particular sex had been sampled and the next sample was a member of that same sex, then that individual was discarded and a new individual was sampled from the same grid cell. If no previously unsampled individuals with the desired sex were present in the grid cell, a new grid cell was chosen. In the event that it was not possible to sample 69 males and 31 females, the O-ring genetic correlation was not performed.

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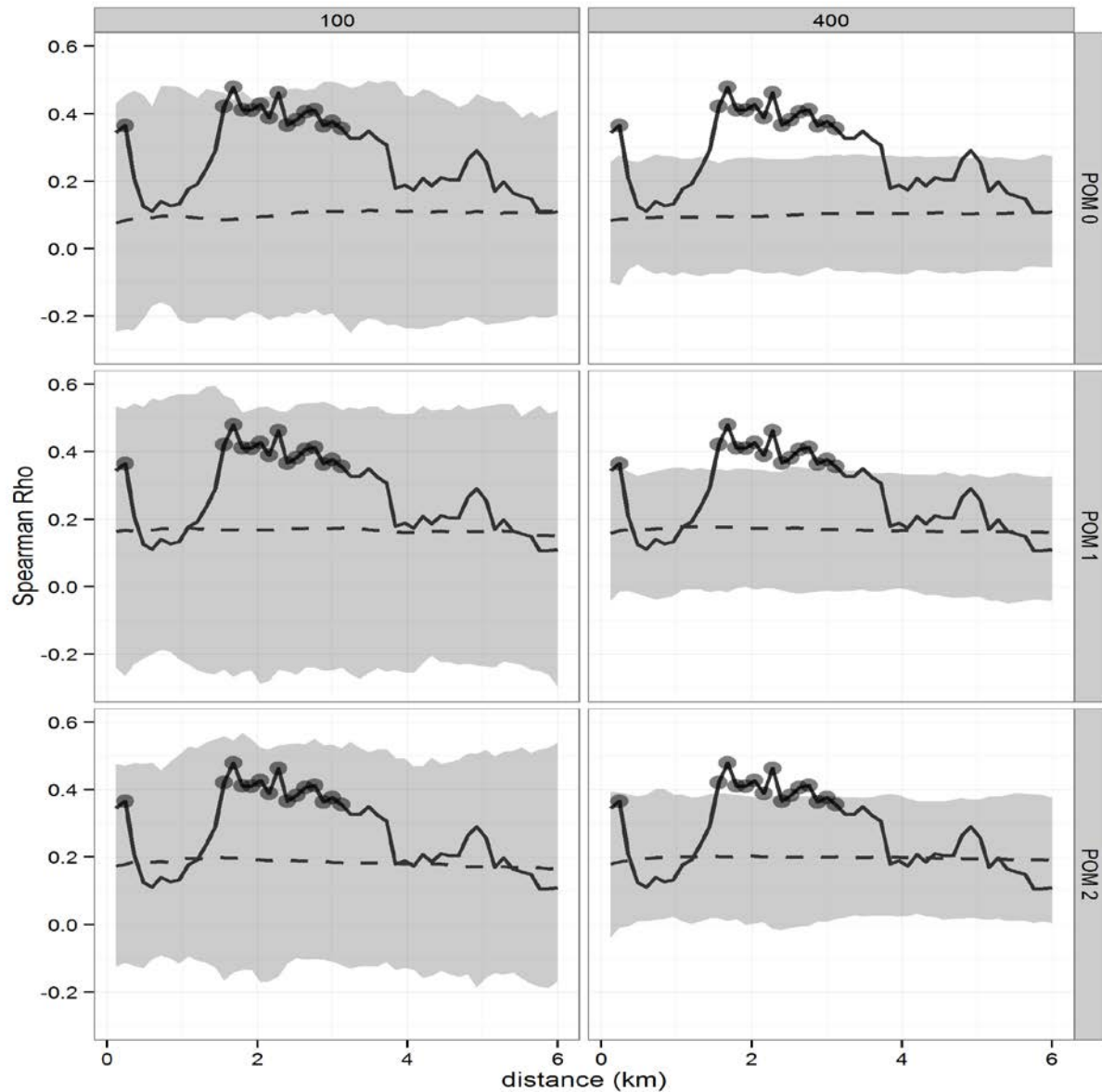


Figure C11. Spearman correlation values (Rho) for females describing the relationship between total number of alleles and O-ring statistics that represent the density of habitat within rings with a width of 120 m. Rings were applied to the landscape at lag distances from 120 m to 6 km, and the correlations are reported for each lag distance. Solid black line represents correlations estimated from empirical genetic samples collected on Ft. Benning (69 males & 31 females), where the dots on that line represent statistical significant correlations ($p < 0.05$). Black dotted line represent mean correlation values estimated from the simulation, and the gray represents 95th percentiles of the distribution of results. We were unable to sample the exact locations in the simulation as that chosen in the field, so random samples of 100 (69 males & 31 females) and 400 (276 males & 124 females) were selected by applying the same sampling grid as was used in the field. Results are presented for the 3 best parameterizations from POM (POM 0, 1, 2) as applied in longPOM.

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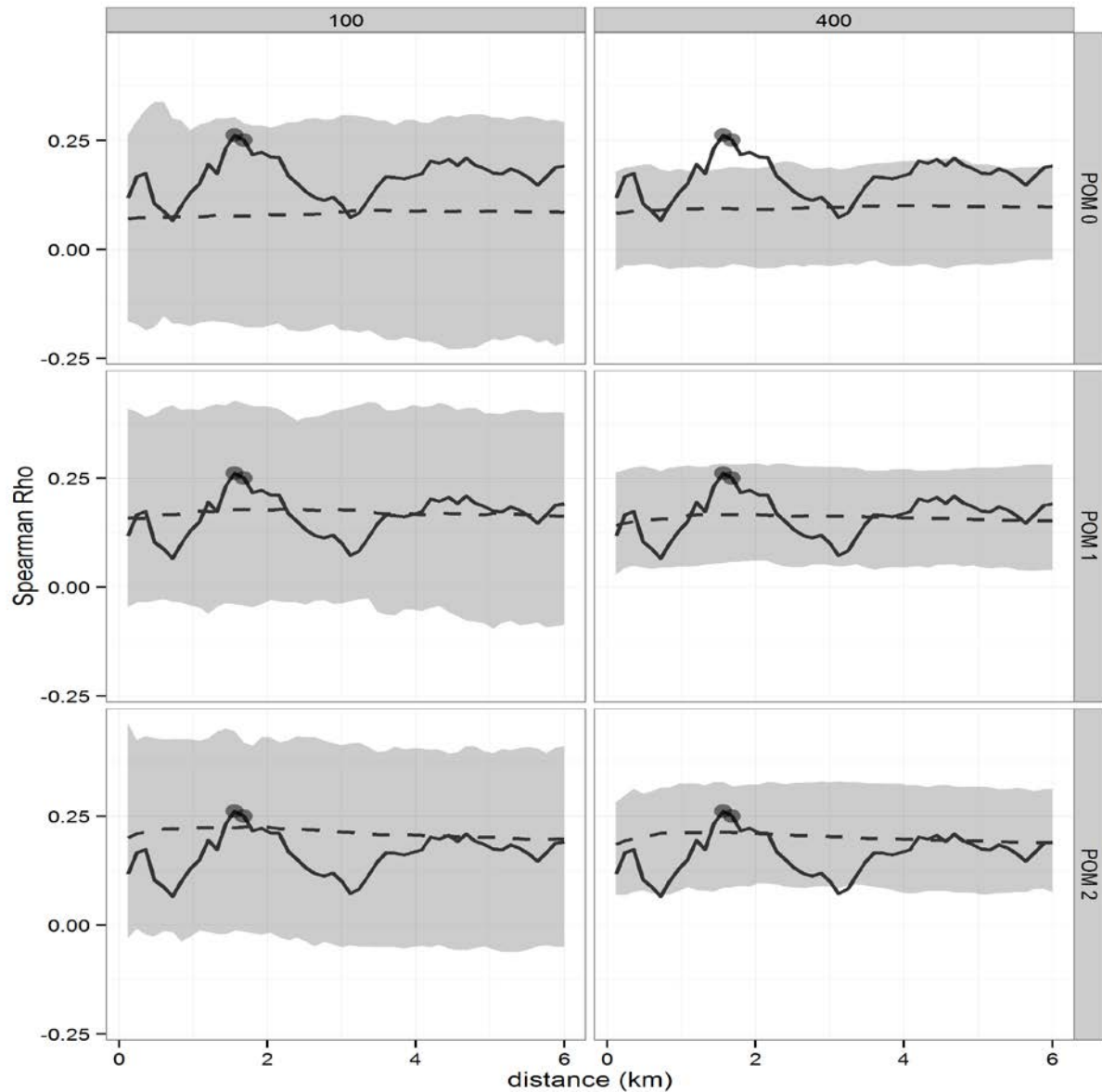


Figure C12. Spearman correlation values (Rho) for males describing the relationship between total number of alleles and O-ring statistics that represent the density of habitat within rings with a width of 120 m. Rings were applied to the landscape at lag distances from 120 m to 6 km, and the correlations are reported for each lag distance. Solid black line represents correlations estimated from empirical genetic samples collected on Ft. Benning (69 males & 31 females), where the dots on that line represent statistical significant correlations ($p < 0.05$). Black dotted line represent mean correlation values estimated from the simulation, and the gray represents 95th percentiles of the distribution of results. We were unable to sample the exact locations in the simulation as that chosen in the field, so random samples of 100 (69 males & 31 females) and 400 (276 males & 124 females) were selected by applying the same sampling grid as was used in the field. Results are presented for the 3 best parameterizations from POM (POM 0, 1, 2) as applied in longPOM.

For each Monte Carlo iteration, we calculated the O-ring genetic correlation in year 2009 (the last year of the simulation). We then compared the simulated results to the empirical results by calculating the mean sum of squared error. For each Monte Carlo iteration and for each sex, we calculated:

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$$SSq(s)^{OCor} = \sum_{r=1}^R (\rho(r, s)_{obs} - \rho(r, s)_{sim})^2$$

Where $SSq(s)^{OCor}$ is the sum of squared error for sex s , and $\rho(r, s)_{obs}$ and $\rho(r, s)_{sim}$ are the empirical and simulated values of the Spearman O-ring genetic correlation for lag distance r (out of a total of R ring sizes) and for sex s . As mentioned above, if 69 males and 31 females were not sampled during a Monte Carlo replicate, for example due to small population size, then the O-ring genetic correlation was not calculated; nor was $SSq(s)^{OCor}$ calculated. To obtain the average $SSq(s)^{OCor}$ value for a parameterization, $SSq(s)^{OCor}$ was averaged across Monte Carlo replicates after excluding replicates where the sampling requirements weren't met.

6B. LEA APPROACH: DISPERSAL PARAMETERS SELECTED FROM POM

Table C5. Dispersal parameters used to evaluate alternative landscape scenarios. The three parameterizations with the minimum sums of squared errors for home range and genetic summary statistics were selected from POM (POM0, POM1, POM2). For all parameter units and definitions, see Table C6.

	POM0	POM1	POM2
Juvenile emigration	0.2	0.2	0.4
Juv. minimum steps	40.6	100	1
Juv. maximum steps	160.4	180.2	180.2
Juv. β	0	0.8	0.8
Subadult M emigration	0	0.2	0
Subadult M minimum steps	40.6	60.4	1
Subadult M maximum steps	120.8	140.6	140.6
Adult and subadult M β	0.4	0.6	0.4
F site philopatry	1	1	1
M mate fidelity	0	0	0

7. SUBMODELS

For parameter definitions, values and sources for all submodels, see Table C6.

Mortality

Lifestage-specific mortality rates are applied in a stochastic manner (i.e., each tortoise is subject to a fixed probability of mortality according to its lifestage). For each tortoise, mortality occurs if a random number sampled from a $u[0,1]$ distribution is less than or equal to the probability of mortality for its corresponding lifestage.

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Update Burrows

Burrows that were occupied by at least one tortoise in the previous year are assigned active status. If a burrow was not occupied by any tortoises in the previous year, its status is changed to abandoned. A burrow that is unoccupied for five years in a row is assumed to collapse, and is removed from the landscape. In surveys, burrows are usually classified as “active”, “inactive”, or “abandoned” (Mushinsky and McCoy 1994). Given that the time step of the model is a year, we cannot distinguish between active and inactive burrows, and instead we lump them together as active.

After long-abandoned burrows are removed from the landscape, we check the ratio of adult, subadult and juvenile tortoises to burrows. If the ratio is above the level of the conversion factor used to initialize the model (i.e., the occupancy rate of burrows estimated on FB), a global flag is set that allows tortoises to dig new burrows during home range assignment.

Emigration

Each year, juveniles, adults, and subadult males are subject to a lifestage- and sex-specific probability of emigration. The path undertaken during emigration follows a habitat-dependent correlated random walk (Zollner and Lima 1999, Bruggeman and Jones 2008). Tortoises are assigned a number of steps to attempt, drawn from a uniform distribution specified by minimum and maximum values. These minimum and maximum values (e.g., M minimum steps, M maximum steps) are defined separately for each lifestage and separately for adult males and females. Each step represents a transition from one grid cell to an adjacent cell. For adults, a random burrow from their current home range is chosen as the starting cell; for immature tortoises, the starting cell is their current location. The tortoise is assigned a random direction of travel for the first step by choosing a random integer between 1 and 8 (i.e., stepping to one of the 8 cells surrounding the starting cell). For each following step the likelihood of moving to each adjacent cell is calculated from two contrasting sets of rules for dispersal: direction-based versus landscape-based. Under landscape-based dispersal, we assume that the tendency of the tortoise to choose any cell for movement (representing landscape permeability) is positively and linearly related to habitat suitability values (described under Landscape above).

The probability of stepping to each of eight surrounding cells is evaluated as:

$$P[\text{step to cell } i] = \beta \times \left(\frac{m_i}{\sum m} \right) + (1 - \beta) \times d^i$$

where β is a weighting parameter indicating preference to move through high quality habitat over maintaining the current direction; m_i is the landscape value at cell i ; $\sum m$ is the sum of landscape suitability values in the eight surrounding cells; and d^i is a parameter indicating the probability of turning in the direction of cell i (i.e., 0°, 45°, 90°, or 135°; the probability of turning 180° is always zero) relative to the direction of travel in the

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previous step. The probability of stepping to each of the eight cells is transformed to a cumulative probability distribution and compared to a $u[0,1]$ random number to determine the cell that the tortoise steps to (thus incorporating stochasticity in the movement path).

Some landscape features are special-cased during emigration (Figure C13). Habitat quality in the unsurveyed NE impact area cannot be estimated directly, but this area is known to be of high habitat quality (Mark Thornton, Ft. Benning, personal communication). Grid cells within this area are assumed to have habitat suitability equal to the average suitability of cells bordering the impact area (0.334 for the POM landscape; 0.379 for the LEA landscape; 0.486 for the pre-settlement landscape), and tortoises may establish burrows there. The southwest impact area, in contrast, is known to be of low habitat quality. This area, and the urban area that is adjacent to it, is assumed to have habitat suitability of 0. If tortoises end their emigration path in the SW impact area or the urban area, for example under parameterizations enforcing highly direction-based emigration, they may establish burrows there (Figure C13). Other small areas on the landscape where suitability could not be directly estimated because of incomplete soil survey data (see Landscape, Section 2) are assumed to be waterbodies.

There is some evidence that gopher tortoises can cross flowing water (Brode 1959), and population genetic analyses have indicated that only very large waterbodies are a barrier to gopher tortoise movement (Clostio et al. 2012). Therefore we allow tortoises to step across water on FB in the simulation for a maximum of ten steps in the current direction; if at the end of ten steps the tortoise is still in a water cell, it is assumed to die and is removed from the simulation. This creates areas on simulation landscape where tortoises will certainly drown if they are entered during emigration (Figure C13). During the LEA simulation experiment, areas of habitat removal are treated similarly to waterbodies, except that tortoises may traverse them without a limited number of steps; that is, removal areas have habitat suitability of zero and tortoises may not establish burrows there.

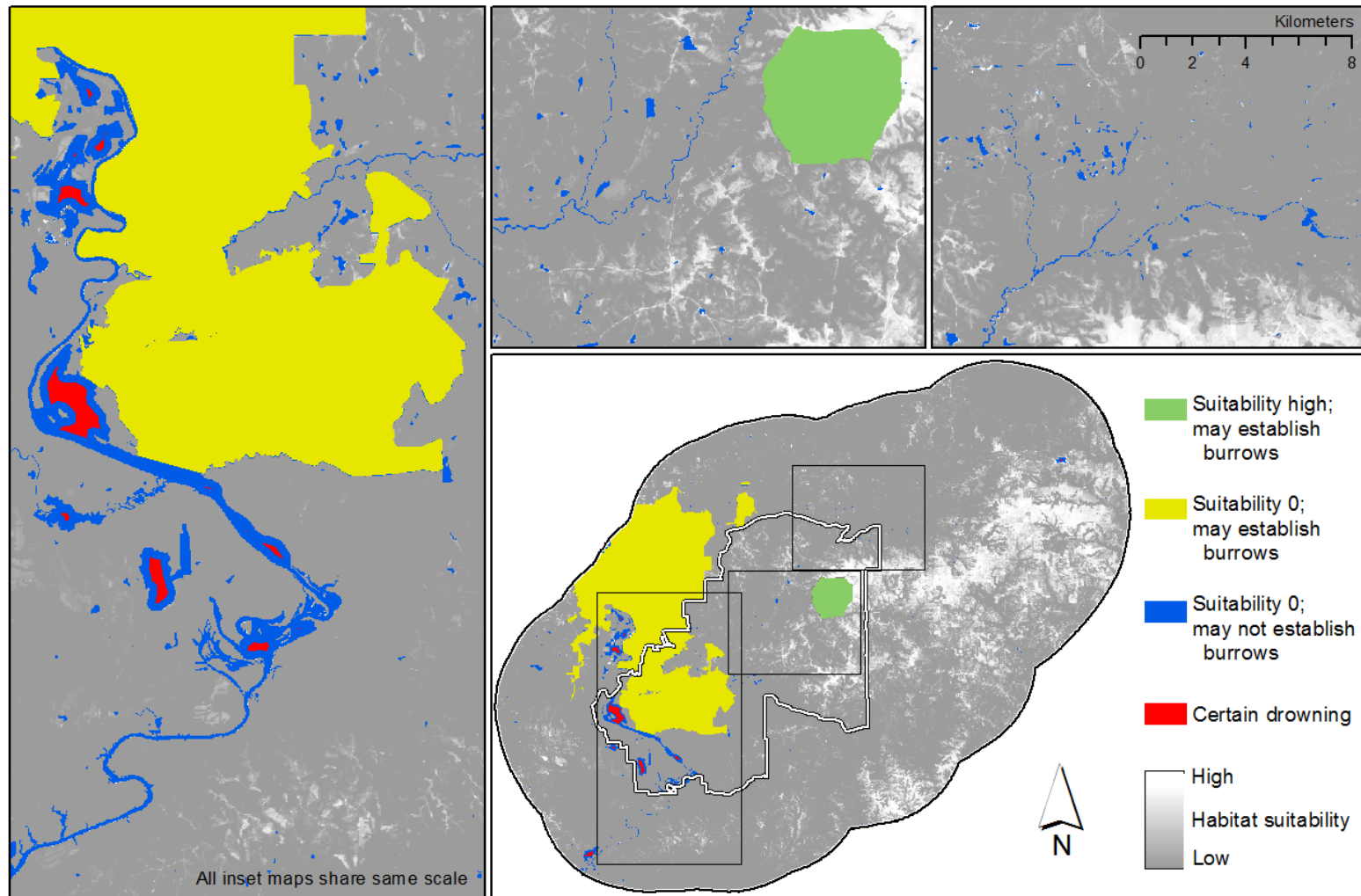


Figure C13. The simulation landscape showing different treatment of areas in emigration. The habitat suitability model for LEA is shown here for illustration; suitability values for the POM and the pre-settlement landscapes are similar. Tortoises may establish burrows in the NE impact area (green) which is assumed to have high habitat suitability (defined as the mean suitability score of cells bordering the impact area; 0.334 for the POM landscape; 0.379 for the LEA landscape; 0.486 for the pre-settlement landscape). Tortoises may establish burrows in the southwest impact area or urban area (both yellow), but these areas are assumed to have habitat suitability of 0. Tortoises may not establish burrows in water (blue) but they may traverse it up to ten steps, after which point they drown. Red areas are greater than ten steps within the boundaries of water, where emigrating tortoises will certainly drown. Note that because tortoises maintain their current direction when they enter the water, it is possible that emigrants would also drown in other water areas.

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After a tortoise has completed at least 80% of its allotted steps, it may end its emigration path early if certain stopping conditions are met. Adult females and immature tortoises are sensitive to habitat suitability: if the habitat suitability of the current cell is above a threshold value (defined as the median suitability value in cells where surveyed burrows were present; 0.323 for the shortPOM landscape; 0.551 for the LEA landscape; 0.678 for the pre-settlement landscape), the tortoise will end its emigration path there. Adult males are sensitive to the proximity of adult females: if there are burrows within a 5-cell radius of the current cell that are occupied by females, the male will end his emigration path at the current cell.

When a tortoise ends its emigration path, either because a stopping condition is met or because it has reached the end of its allotted steps, it first checks for existing burrows within a 5-cell radius of the ending cell. If there are burrows present, one of them is chosen at random and becomes the focal burrow around which the home range is assigned (detailed under home range assignment submodels below). If no existing burrows are available, the tortoise digs 1-2 burrows and the home range is assigned around one of those burrows.

Assign home range

Field observations suggest that male tortoises have some awareness and memory of the locations of females, and travel to burrows occupied by females to court and mate there (Boglioli et al. 2003, Johnson et al. 2009, Guyer et al. 2012). We simulate this behavior by allowing individuals to mate only when their home ranges overlap. We assume that a greater degree of overlap (i.e., more burrows in common between two individuals) confers a greater probability of successful mating, and therefore a simulated male that has many burrows in common with a female experiences a higher likelihood of siring the offspring of that female.

Because home range size in the field differs depending on the local density of burrows (Guyer et al. 2012), we limit home range size using an “energy budget” calculated as the sum of all pairwise distances between burrows in the home range. When adding burrows to their home range, tortoises are less likely to add burrows that are already occupied by another tortoise of the same sex (Johnson et al. 2009, Guyer et al. 2012). If the global flag is set to allow new burrows to be created (i.e., the ratio of tortoises to burrows is too high; see Update burrows submodel), tortoises may dig new burrows to add to their home range. Because immature tortoises are not known to participate in social interactions (McRae et al. 1981, Diemer 1992a), their home range is not explicitly modeled until they become adults.

Assign female home range

Adult females are assigned a home range using the following process at the initialization of each Monte Carlo iteration, when they mature to adulthood, and at the end of an emigration path. If the binary parameter that enforces female site philopatry is in effect, the following process is only used to assign the initial home range

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and females continue to occupy the same burrows throughout their lifespan. If the female site philopatry parameter is not in effect, the home range of each female is reassigned each year starting at a burrow of the previous year selected randomly. Pseudocode of the female home range assignment submodel is provided below.

```
Choose random start burrow
Obtain energy budget from sex-specific distribution
Search radius = 0
While sum of pairwise distances in HR < energy budget and search radius <= maximum radius {
  For each burrow in search radius, accessed randomly {
    Probability of adding burrow = base probability
    If burrow is occupied by another female {
      Probability of adding burrow = base probability × aversion parameter
      p = random float in u [0,1]
      if p < probability of adding burrow {
        add burrow
        recalculate sum of pairwise distances in HR
      }
    }
  }
  Increment search radius
}

If search radius = maximum radius and sum of pairwise distances in HR < energy budget {
  While sum of pairwise distances in HR < energy budget {
    Dig burrows
  }
}
```

Assign male home range

The male home range assignment process is similar to that for females, but because males are known to occupy larger home ranges than females (McRae et al. 1981, Diemer 1992a, Smith et al. 1997, Guyer et al. 2012), all home range assignment parameters are estimated separately for the two sexes. The two submodels also differ in that males are motivated to share burrows with females. For this reason, the Assign female home range submodel is always called before the Assign male home range submodel.

In addition to an aversion parameter that causes males to avoid members of the same sex, we also include parameters that alter the probability that a male adds a burrow to his home range depending on the females that occupy that burrow. If the binary parameter enforcing male mate fidelity is in effect, males are motivated to overlap with females that they overlapped with in the previous year. If the male mate fidelity parameter is not in effect, or if the male did not overlap with any females in the previous year, the male is motivated to overlap with as many different females as possible. After the home range of a male tortoise is assigned, copies of the male's genetic material are added to the sperm storage of females that he overlaps with, in proportion to the number of

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burrows that they both occupy. Pseudocode of the male home range assignment submodel follows.

```
Choose random start burrow
Obtain energy budget from sex-specific distribution
Search radius = 0
fOverlap = females that he overlaps with
While sum of pairwise distances in HR < energy budget and search radius <= maximum radius {
  For each burrow in search radius, accessed randomly {
    Probability of adding burrow = base probability

    Modify probability of adding burrow according to current occupants:
    If male mate fidelity parameter is in effect AND he overlapped with females in the previous year {
      If burrow is occupied by female that he overlapped with in previous year {
        Probability = 1
      }
    }
    else (male mate fidelity is not in effect, OR he did not overlap with females in the previous year) {
      If burrow is occupied by another male
        Probability of adding burrow = base probability  $\times$  aversion parameter
      If burrow is occupied by any females
        Probability = probability  $\times$  female-occupied parameter
      If burrow is occupied by new females not in fOverlap
        Probability = probability  $\times$  new female parameter
    }

    p = random float in [0,1]
    if p < probability of adding burrow {
      add burrow
      add all females occupying that burrow to fOverlap
      recalculate sum of pairwise distances in HR
    }
  }
  Increment search radius
}
For each female in fOverlap {
  For each burrow that he has in common with that female {
    Add one copy of this male's genetic material to sperm storage of that female
  }
}

If ending search radius = maximum radius and sum of pairwise distances in HR < energy budget {
  While sum of pairwise distances in HR < energy budget {
    Dig burrows
  }
}
```

Dig burrows (submodel of assign home range submodels)

Tortoises are allowed to dig new burrows when the global flag allowing new burrows is set (see Update Burrows submodel) and when they have not added enough existing burrows within the maximum search radius to meet

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their allotted energy budget (see Assign Home Range submodels). This submodel is also employed when tortoises are relocated to pens. In both cases, the placement of new burrows is constrained by two factors: new burrows are only added in areas where the habitat suitability is above a threshold value (defined as the median suitability value in cells where surveyed burrows were present; 0.323 for the shortPOM landscape; 0.551 for the LEA landscape; 0.678 for the pre-settlement landscape), and at a realistic distance from existing burrows. Examination of nearest neighbor distances in surveyed burrows (i.e., the 1999 and 2008 surveys of FB) revealed that the majority of burrows (79% in the 1999 survey, and 71% in the 2008 survey) were located within two grid cells of another burrow, but that it was extremely rare ($< 1\%$ of grid cells for both surveys) for grid cells to contain more than two burrows. Therefore when burrows are added in POM and LEA mode, their location is restricted to be within two grid cells of an existing burrow and in a grid cell containing less than two burrows.

Because of the greater density of burrows on the pre-settlement landscape, for this landscape burrows are allowed to be added in a more densely packed fashion. Burrows added to the pre-settlement landscape are restricted to be added within one grid cell of an existing burrow, and in a grid cell containing less than three burrows.

Reproduction

Female gopher tortoises are known to store sperm from males they have mated with, potentially for several years (Palmer and Guillet 1988, Pearse and Avise 2001). In the simulation, the sperm storage of adult females tracks the number of matings with different males over the past three years. Each year, entries in the sperm storage container of each adult female are cleared if they are more than three years old. Then if an adult female possesses any entries in her sperm storage (i.e., if she shared at least one burrow with at least one male over the last three years), she attempts to lay a clutch of eggs. The number of eggs in the clutch is drawn randomly from a normal distribution, and the father for each egg is chosen by drawing randomly with replacement from the sperm storage. In this way, males that shared more burrows with the female (and thus contributed proportionally more entries to the sperm storage) have a greater likelihood of siring offspring. A random burrow from the female's current home range is chosen as the natal site for the clutch. The clutch is stochastically subjected to a fixed probability of total nest predation; then, if the nest is not destroyed, each egg is subjected to a fixed probability of hatching successfully. If the egg hatches successfully, the new tortoise receives alleles drawn randomly from those of the mother and father. We enforce a 1:1 sex ratio at conception (Douglass and Layne 1978, Berish et al. 2012).

Population genetic statistics

POM Approach. We calculate the total number of alleles (TNA) per individual as the total number of unique alleles present at each of the 31 microsatellite loci. This value is correlated with O-ring statistics describing the

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spatial autocorrelation of habitat to provide a summary statistic for POM.

LEA Approach. We calculate total expected heterozygosity (H_t ; Nei 1973) and Wright's inbreeding coefficient F . Under an Infinite Alleles Model, Wright's inbreeding coefficient, the probability that two alleles chosen at random from within a breeding group are identical by descent, was estimated as $F = 1 - H_o$ (Miller and Lacy 2005), where H_o equals the average observed frequency of heterozygous individuals at the IAM locus within the population.

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Table C6. Parameter values, definitions and sources.

Parameter	Definition	Units	Constant/Uncertain	Constant value	Source
Initialization					
Conversion factor	Ratio of adult, subadult and juvenile tortoises to adult active and inactive burrows	Ratio	Constant	0.327	Staff of Fort Benning Conservation Branch 2012
Mortality					
Hatchling mortality	Probability of hatchling mortality (each year)	Probability	Constant	0.872	Butler and Sowell 1996, Epperson and Heise 2003, Pike and Seigel 2006, Perez-Heydrich et al. 2012
Juvenile mortality	Probability of juvenile mortality (each year)	Probability	Constant	0.3	Wilson 1991, Tuberville et al. 2008
Subadult mortality	Probability of subadult mortality (each year)	Probability	Constant	0.015	Ashton and Burke 2007, Tuberville et al. 2008
Adult mortality	Probability of adult mortality (each year)	Probability	Constant	0.015	Ashton and Burke 2007, Tuberville et al. 2008, Ozgul et al. 2009
Juvenile duration	Duration of subadult lifestage	Years	Constant	3	Landers et al. 1982
Age at maturity	Age at sexual maturity (males and females)	Age	Constant	18	Diemer and Moore 1994, Landers et al. 1982
Maximum age	Age at forced mortality	Age	Constant	55	Landers et al. 1982
Reproduction					
Nest predation	Probability of nest predation	Probability	Constant	0.71	Smith et al. 2013, Diemer and Moore 1994, Landers et al. 1980
Pre-settlement nest predation	Probability of nest predation in pre-settlement time	Probability	Constant	0.648	ESaM professional judgment
Successful hatch	Probability of an egg hatching successfully	Probability	Constant	0.79	Landers et al. 1980, Butler and Hull 1996, Demuth 2001, Rostal and Jones 2002, Epperson and Heise 2003, Moon et al. 2006, Tuberville et al. 2011
Clutch mean	Mean number eggs per clutch	Eggs	Constant	7	Landers et al. 1980, Iverson 1980, Diemer and Moore 1994, Butler and Hull 1996, Smith et al. 1997, Demuth 2001, Rostal and Jones 2002, Epperson and Heise 2003, Moon et al. 2006, Pike and Seigel 2006, Ashton et al. 2007, Tuberville et al. 2011
Clutch standard deviation	Standard deviation of eggs per clutch	Eggs	Constant	1.7	Same as clutch mean
Clutch minimum	Minimum number of eggs per clutch	Eggs	Constant	0	Same as clutch mean
Clutch maximum	Maximum number of eggs per clutch	Eggs	Constant	12	Same as clutch mean

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Parameter	Definition	Units	Constant/ Uncertain	Constant value	Range	Source
Home range assignment						
F energy budget mean	Maximum allowable sum of pairwise distances between burrows in home range	Grid cells	Constant	55	NA	Analysis of Guyer telemetry dataset at low-density sites: average sum of pairwise distances between burrows in home range
F max distance	Maximum search radius for burrows in home range	Grid cells	Constant	27	NA	Analysis of Guyer telemetry dataset at low-density sites: maximum distance observed to outlying burrows in home range
F add burrow	Probability of adding a burrow to home range (female)	Probability	Constant	0.7	NA	ESaM professional judgment
F aversion	Decrease in probability of adding burrow if currently occupied by another female	Multiplication factor	Constant	0.5	NA	ESaM professional judgment
M energy budget mean	Maximum allowable sum of pairwise distances between burrows in home range	Grid cells	Constant	90	NA	Analysis of Guyer telemetry dataset at low-density sites: average sum of pairwise distances between burrows in home range
M max distance	Maximum search radius for burrows in home range	Grid cells	Constant	27	NA	Analysis of Guyer telemetry dataset at low-density sites: maximum distance observed to outlying burrows in home range
M add burrow	Probability of adding a burrow to home range (male)	Probability	Constant	0.7	NA	ESaM professional judgment
M aversion	Decrease in probability of adding burrow if currently occupied by another male	Multiplication factor	Constant	0.2	NA	ESaM professional judgment
M add shared burrow	Increase in probability of adding burrow if currently occupied by a female	Multiplication factor	Constant	1.5	NA	ESaM professional judgment
M add shared new	Increase in probability of adding burrow if currently occupied by a "new" female	Multiplication factor	Constant	5	NA	ESaM professional judgment
F site philopatry	Females use same burrows each year (1) or shift home range each year (0)	Binary	Uncertain	0	0 : 1	ESaM professional judgment
M mate fidelity	Males are motivated to overlap with same females as previous year (1), or are not (0)	Binary	Uncertain	0	0 : 1	ESaM professional judgment

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Parameter	Definition	Units	Constant/ Uncertain	Constant value	Range	Source
Emigration						
F emigration	Probability that adult female will emigrate (each year)	Probability	Constant	0.02	NA	Diemer and Moore 1993, Berish et al. 2012
F minimum steps	Minimum number of steps to undertake	Grid cell transitions	Constant	30	NA	Diemer and Moore 1993, Berish et al. 2012
F maximum steps	Maximum number of steps to undertake	Grid cell transitions	Constant	50	NA	Diemer and Moore 1993, Berish et al. 2012
F habitat β	Weighting parameter: tendency to follow quality habitat over maintaining direction	–	Constant	0.8	NA	ESaM analysis of Ft. Benning genetic structure
M emigration	Probability that adult male will emigrate (each year)	Probability	Constant	0.035	NA	McRae et al. 1981, Eubanks et al. 2003
M minimum steps	Minimum number of steps to undertake	Grid cell transitions	Constant	40	NA	McRae et al. 1981, Eubanks et al. 2003
M maximum steps	Maximum number of steps to undertake	Grid cell transitions	Constant	200	NA	McRae et al. 1981, Eubanks et al. 2003
Subadult male emigration	Probability that subadult male will emigrate (each year)	Probability	Uncertain	0.01	0 – 1	Diemer and Moore 1993, Diemer 1992
Subadult male minimum steps	Minimum number of steps to undertake	Grid cell transitions	Uncertain	7	1 – 100	Diemer and Moore 1993, Diemer 1992
Subadult male maximum steps	Maximum number of steps to undertake	Grid cell transitions	Uncertain	25	101 – 200	Diemer and Moore 1993, Diemer 1992
Adult and subadult male habitat β	Weighting parameter: tendency to follow quality habitat over maintaining direction	–	Uncertain	0.2	0 – 1	ESaM analysis of Ft. Benning genetic structure
Juvenile emigration	Probability that juvenile will emigrate (each year)	Probability	Uncertain	0	0 – 1	ESaM professional judgment
Juv. minimum steps	Minimum number of steps to undertake	Grid cell transitions	Uncertain	0	1 – 100	ESaM professional judgment
Juv. maximum steps	Maximum number of steps to undertake	Grid cell transitions	Uncertain	0	101 – 200	ESaM professional judgment
Juv. habitat β	Weighting parameter: tendency to follow quality habitat over maintaining direction	–	Uncertain	0	0 – 1	ESaM professional judgment
D ^{0°}	Probability of maintaining direction of travel in previous step	Probability	Constant	0.8	NA	ESaM professional judgment
D ^{45°}	Probability of turning 45° from direction of travel in previous step	Probability	Constant	0.08	NA	ESaM professional judgment
D ^{90°}	Probability of turning 90° from direction of travel in previous step	Probability	Constant	0.02	NA	ESaM professional judgment
D ^{135°}	Probability of turning 135° from direction of travel in previous step	Probability	Constant	0	NA	ESaM professional judgment
Subadult radius	Radius around natal or current site at which tortoises are introduced onto the landscape as adults	Grid cells	Constant	15	NA	Diemer 1992a, Wilson et al. 1994, Butler et al. 1995, Epperson and Heise 2003, Pike 2006
Landscape friction	Substrate determining landscape permeability/resistance to movement	–	Constant	Habitat suitability	NA	Clostio 2010, ESaM professional judgment

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Appendix D: List of Scientific/Technical Publications

Peer-reviewed Publications

Bruggeman, D. J. 2008. Possibility of common currency for tradable credit systems. *Endangered Species Update* 25:12-14.

Bruggeman, D. J., and M. L. Jones. 2008. Should habitat trading be based on mitigation ratios derived from landscape indices: a model-based analysis of compensatory restoration options for the Red-cockaded woodpecker. *Environmental Management* 42: 591-602.

Bruggeman, D. J., M. L. Jones, K. Scribner, and F. Lupi. 2009. Relating tradable credits for biodiversity to sustainability criteria in a dynamic landscape. *Landscape Ecology* 24: 775-790.

Bruggeman, D. J., T. Wiegand, and N. Fernandez. 2010. The relative effects of habitat loss and fragmentation on population genetic structure of the Red-cockaded Woodpecker (*Picoides borealis*). *Molecular Ecology* 19: 3679-3691.

Kreiser, B. R., J. R. Ennen, D. L. Gaillard, and C. P. Qualls. 2013. Isolation and characterization of polymorphic microsatellite loci for the gopher tortoise (*Gopherus polyphemus*) and cross-amplification in other species of *Gopherus*. *Conservation Genetics Resources* 5:255–259

Kowal V. A., A. R. Schmolke, Kanagaraj, D. J. Bruggeman. In press. Informing Management of a Threatened Species: Defining Habitat Suitability for Gopher Tortoise. *Environmental Management*

Bruggeman, D. J., T. Wiegand, J. Walters, F. Gonzalez. In press. Contrasting the ability of data to make inferences regarding dispersal for the Red-cockaded Woodpecker (*Picoides borealis*). *Landscape Ecology*

Bruggeman, D. J., P. Hartger, J.R. Walters, J. Wagaman. In prep. The influence of climate and demography on recruitment in the Red-Cockaded Woodpecker.

Bruggeman, D.J. In prep. Application of Decision Analysis to Landscape-scale Biodiversity Credit Systems.

Kowal, VA, MR Robison, DJ Bruggeman. In prep. Development and testing of individually-based, spatially-explicit population model for the Gopher Tortoise.

Robison, MR, DJ Bruggeman, D. Gaillard. In prep. Fine scale landscape genetic patterns in the gopher tortoise (*Gopherus polyphemus*).

Presentations / Published Abstracts

Ecological Society of America. Minneapolis, August 2013. Learning from models: individual-based models inform field data collection priorities for the Gopher Tortoise. VA Kowal, D Bruggeman, M Robison, and A Schmolke

USDA Office of Environmental Markets (Invited). April 30, 2013. Application of Adaptive Management to Landscape-scale Tradable Credit Systems for At-Risk Species. D. Bruggeman

EcoSummit. Columbus, Ohio. October 1, 2012. Co-Chaired Symposium: Landscape-scale Tradable Credit Systems for Biodiversity. D. Bruggeman and S. Whitten.

EcoSummit. Columbus, Ohio. October 1, 2012. Application of Decision Analysis to Landscape-scale Biodiversity Credit Systems. D. Bruggeman

Ecological Society of America. Portland, August 2012. Habitat suitability for gopher tortoises. A Schmolke, VA Kowal, R Kanagaraj and D Bruggeman.

CSIRO, Canberra, Australia (Invited). December 12, 2011. Relating Tradable Credits for Biodiversity to Sustainability Criteria in a Dynamic Landscape. D. Bruggeman

International Congress for Conservation Biology. Auckland, New Zealand. December 8, 2011. Incorporating the Influence of Uncertainty into Biodiversity Credit Systems. D. Bruggeman and T. Wiegand.

Ecological Society of America. Austin, TX. August 7-12, 2011. Contrasting information content of demographic and genetic data when inversely estimating dispersal parameters. D. Bruggeman, T. Wiegand, J. Walters, F. Gonzalez.

US Society for Ecological Economics. East Lansing MI. June 26-29, 2011. Incorporating the influence of uncertainty in biodiversity credit systems. D. Bruggeman, & T. Wiegand.

International Society for Ecological Economics. Oldenburg, Germany. August 23-25, 2010. Incorporating the influence of uncertainty in biodiversity credit systems. D. Bruggeman, & T. Wiegand.